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CULTURE TYPES AND PATHOGENICITY OF ISOLATES OF CORTICIUM SOLANI[1]

BYRON R. HOUSTON[2,3]

(Accepted for publication October 9, 1944)

INTRODUCTION

The fungus *Corticium solani* (Prill. and Del.) Bourd. and Galz. (*C. vagum* Berk. and Curt.) (*Rhizoctonia solani* Kühn) is known to be present in all parts of the world where its host plants are extensively grown. In California it causes serious losses in many of the common commercially grown crops including alfalfa, bean, cotton, cowpea, potato, and sugar beet. With the use of these crops in a system of rotation, it becomes important to know the specialization in relation to pathogenicity within the strains of this fungus.

This investigation was undertaken to increase our knowledge of the parasitism and cultural characters of isolates of the fungus obtained from agriculturally important hosts.

At present the species *Corticium solani* includes a group of fungi heterogeneous in nature with reference to their growth characters and their ability to produce disease. Studies of the morphologic characters of *C. solani* by Duggar (9), Le Clerg (16), Matsumoto (20), and Rosenbaum and Shapovalov (31) have shown that there may be slight or occasionally somewhat more pronounced morphologic differences between individual isolates. However, for the separation of cultural types the most desirable method found in this investigation was to use the differences shown by the isolates in their growth characters, pathogenicity, and physiology. In his textbook on diseases of plants, Julius Kühn in 1858 described and named *Rhizoctonia solani* as a fungus causing a disease of potatoes and thus distinguished it from the species *R. violacea* with which it apparently had been previously combined. An extensive review of early literature has been given by Duggar (9) and Peltier (24) and will not be included here.

Investigations on racial specialization have been undertaken by several workers including Duggar (9), Edson and Shapovalov (12), Gratz (13), Le Clerg (17, 18, 19), Matsumoto (20), Monteith and Dahl (21), Peltier (24), Sanford (32, 33), and Storey (34). In 1915 Duggar (9) made an elaborate study of the common *R. solani* and concluded that there was little marked specialization. Peltier (24) found no outstanding strain specialization in pathogenicity but noted differences in cultural characters. In 1917 Rosenbaum and Shapovalov (31) identified a new strain of *Rhizoctonia*

[1] The work herein reported was part of a thesis presented to the Graduate School of the University of California, September, 1939, in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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[3] The writer wishes to acknowledge his indebtedness to Dr. M. W. Gardner for his advice and criticism throughout these investigations and for editing the manuscript.

occurring on potato on the basis of the type of lesions produced by it on the potato stems, its growth and sclerotial characters, and the different cell size noted when it was compared with their other isolates from potato. Matsumoto (20) in 1921 separated isolates of *R. solani* into several strains and suggested a possible specific rank for one of them. Le Clerg (16) first reported pathogenically distinct strains on potato and sugar beet; however, he later found (17, 18, 19) that some potato isolates were pathogenic to sugar beet and that most sugar-beet isolates were pathogenic upon potatoes. Storey (34) reported that some strains had a wide host range whereas others possessed a more selective parasitism.

From the investigations of Müller (22), Prillieux and Delacroix (25), Rolfs (29), Ullstrup (35) and others, it can be concluded that there is a definite connection between the vegetative stage, *Rhizoctonia solani,* and the perfect stage, *Corticium solani,* so the latter name should be used in preference to the former.

The correct nomenclature of this fungus has long been in controversy. The English and American pathologists have used the name *Corticium vagum* Berkeley and Curtis, whereas the continental European workers refer to the same fungus as *Corticium solani* Prillieux and Delacroix. The name *Rhizoctonia solani* Kühn is still commonly used in the literature.

In 1891 Prillieux and Delacroix (25) reported the occurrence of the basidial stage of a fungus on potato stems. The white mycelial growth, which could be easily removed, extended up the stem for several centimeters and did not penetrate the epidermis. This mycelial mat produced basidia, each with four sterigmata bearing smooth hyaline basidiospores. Under the system of classification used by them, the fungus was named *Hypochnus solani,* a new species, but they did not at that time connect this stage with the vegetative stage of the fungus, *Rhizoctonia solani.* However, from their drawings, descriptions, and measurements, it appears they were working with this organism.

Rolfs (29) observed the basidial stage of this fungus in 1903 on the leaves and stems of potatoes while working with the Rhizoctonia disease. He was able to germinate the spores and prove the connection between this stage and the vegetative stage pathogenic on the tubers and stems. He sent specimens of this fungus to Burt at the Missouri Botanical Gardens who referred it to *Corticium vagum* Berkeley and Curtis which had been described by the English mycologist Berkeley (2) in 1873. This name was originally applied by Berkeley to a specimen of a saprophytic fungus producing basidiospores on a thin hymenial layer on pine bark sent to him by Curtis from South Carolina. No connection between this and the vegetative state *R. solani* was proven. Burt (5), in comparing this with the specimen from Rolfs, noticed slight differences in the size and shape of the basidiospores, and thus named Rolf's fungus *C. vagum* B. and C. var. *solani* Burt. Vegetative stages of the two were not compared at this time. Rolfs accepted Burt's classification of the fungus and *Hypochnus solani* became a synonym. Most

American and English workers have accepted this until rather recently. In continental Europe the name *Hypochnus solani* was accepted until 1911 when Bourdot and Galzin (3) recognizing the difference in the systems of nomenclature used by Prillieux and Delacroix and by Burt (5) made the new combination *Corticium solani*. This latter name is now preferred by English and some American mycologists as well as by those in continental Europe, and also was used by Weiss (37) in his revision of the Check List of Diseases of Economic Plants in the United States. The complete citation, *Corticium solani* (Prill. and Del.) Bourd. and Galz., as suggested by Weiss, seems to be the correct one to use for this fungus. Recently, however, Rogers (28) has included *Corticium solani* and several other related fungi under the binominal *Pellicularia filamentosa* (Pat) Rogers.

SOURCE OF ISOLATES

With differences occurring between isolates from the different hosts and even between those from the same host, it is necessary, in order to study differences, that many isolations be made from each important host. The 52 isolates listed in table 1 and used in this study were obtained primarily from California and were selected from 260 isolations from 15 different crop plants in widely separated regions of the State. The placing of the isolates in the cultural groups A, B, and C is discussed in the following section. In the selection of the isolates a careful comparison of cultural characters was made of those from the same host and same locality, and only those with differences were selected. Also, preliminary pathogenicity trials were made on all isolates, and those from the same immediate locality, unless they appeared very different in culture, were found to have the same degree of pathogenicity on the same hosts. In this way, it is felt that a representative group from the more important hosts was selected. Before attempting a comparison of the isolates, pure cultures of each were assured by obtaining hyphal-tip cultures. All isolates having the prefix number 24 were hyphal tip cultures and all those having the prefix number 35 were single or multiple basidiospore cultures.

CULTURAL CHARACTERS

When growing on an agar medium there were some striking growth differences which were used to separate the isolates into several groups. Matsumoto (20) used the intensity of the darkening of the culture medium as a basis on which to separate the isolates studied by him into three groups. However, since this character is variable depending upon the type of culture medium employed and the environmental conditions, it must not be considered as one of the more important characters of growth. The striking features of growth were the presence or absence of a stroma-like layer of mycelium on the surface of the medium, the color of this layer, the relative amount of aerial mycelium produced, the abundance, type and color of the sclerotia, and the growth rate.

TABLE 1.—*Source and culture types of isolates of Corticium solani used in the pathogenicity trials*

No. and culture type of isolate	Host from which isolated	Effect on host
Type A		
24– 9	Bean, Lima	Stem canker
24–49	Bean, Mung	do
24–52	Bean, Pink	do
24–21	Cotton	Damping off
24–22	do	do
24–29	do	do
24–30	do	do
24–32	do	do
24–18	Cowpea, Blackeye	Stem canker
24–86	do	do
24–82	Fenugreek	Damping off
24–42	Potato	Stem canker
24–14	Rhubarb	Petiole rot
24– 8	Spinach	Damping off
24–85	Squash	Crown rot
24– 1	Sugar beet	Damping off
24–11	do	do
24–15	do	Dry-rot canker
24–35	do	do
24–38	do	do
24–43	do	do
24–48	do	do
24–80	do	do
24–81	do	do
24– 7	Tomato	Damping off
24–83	do	Fruit rot
Type B		
24– 3	Sugar beet	Dry-rot canker
24–17	do	do
24–24	do	do
24–27	do	do
24–34	do	do
24–36	do	do
24–37	do	do
24–40	do	do
24–45	do	do
Type C		
24–84	Alfalfa	Crown rot
24–12	Asparagus	Stem rot
24–76	Bean, Pink	Stem canker
35– 4	Celery	Basidiospore group
24– 4	Potato	Tuber sclerotium
24–13	do	Stem canker
24–19	do	Tuber rot
24–28	do	do
24–51	do	Tuber sclerotium
24–69	do	do
35– 2	do	Basidiospore group
24– 6	Strawberry	Root rot
35– 1	Tomato fruit	Basidiospore group
35– 7	do	Single basidiospore

These characters were studied in 100 isolates growing at a constant temperature of 25° C. on a potato-dextrose agar of pH 6.8. The isolates were rather easily separated into three groups, here designated culture types A, B, and C.

Culture type A was characterized by: (1) a heavy stroma-like layer on the surface of the medium, at first almost white and later becoming Ridgway's (27) pale drab gray to light drab. This surface growth often was convoluted. A light cinnamon drab, multihyphal strand growth may be produced on the surface of this layer; (2) natal brown sclerotia, appearing as slightly raised areas of the surface growth, often radiating out from the point of inoculation and not typically small isolated bodies except those produced where the aerial mycelium grew in contact with the sides of the culture dish. This latter type was typically flat and not globular; (3) aerial mycelium sparse and white to cinnamon; (4) a rapid growth rate (1.0 to 1.8 mm. per hour); (5) often a pronounced darkening of the culture medium.

Culture type B was characterized by: (1) no pronounced stroma-like layer on the surface of the medium; (2) few, natal brown, globular sclerotia, one to four mm. in diameter, and commonly formed by the aerial mycelium when in contact with the sides of the culture dish, or suspended in the air; (3) very abundant aerial mycelium, pale olive buff to sayal brown, and forming a solid mass which usually grew well above the upper portion of the culture medium in a test tube slant; (4) a moderate growth rate (0.6–0.8 mm. per hour); (5) no darkening of the culture medium.

Culture type C was characterized by: (1) a slight stroma-like layer on the surface of the agar, at first vinaceous buff and becoming wood brown with age; (2) sclerotia natal brown, globular, with a very irregular surface, and often united into groups as large as 15 mm. in diameter. Individual sclerotia were one to five mm. in diameter and scattered over the surface growth; (3) aerial mycelium very sparse or lacking; (4) a moderate to slow growth rate (0.5 to 0.7 mm. per hour), (5) none to moderate darkening of the culture medium.

Representative isolates are in figure 1.

Although there were occasional isolates that appeared to be of a type between two of the defined types, as might be expected in such a heterogeneous group of fungi, most isolates could readily be placed in their respective group and this scheme affords an easy and workable means of separation. It seems to be usable for those isolates of *Corticium solani* that are parasitic upon the common commercially grown hosts in California and for all isolations that were made in the course of this study.

THE EFFECT OF TEMPERATURE ON RATE OF GROWTH

The effect of temperature on the rate of mycelial growth of a number of isolates was studied. Petri dishes of uniform size were sterilized and 10 ml. of sterile potato-dextrose agar poured into each dish. Dishes were inoculated with mycelium inoculum obtained by cutting discs 2 mm. in diameter from a point approximately 1 cm. behind the advancing margin of colonies growing on the agar, and placing the discs in the center of the poured dishes. In each of two trials four dishes of each isolate were placed at the following temperatures: 4°, 10°, 16°, 22°, 25°, 28°, 31°, 34°, and 40° C. The more

rapidly growing isolates advanced to the edges of the dishes in about 50 hours, so a 48-hour measurement was used in their comparison.

The isolates could be separated into three groups based upon their average growth rates and their optimum and maximum temperatures. Nine of the twenty-five isolates studied were selected as representative and are shown graphically in figure 2. The isolates 24–1, 24–7, 24–8, 24–9, and

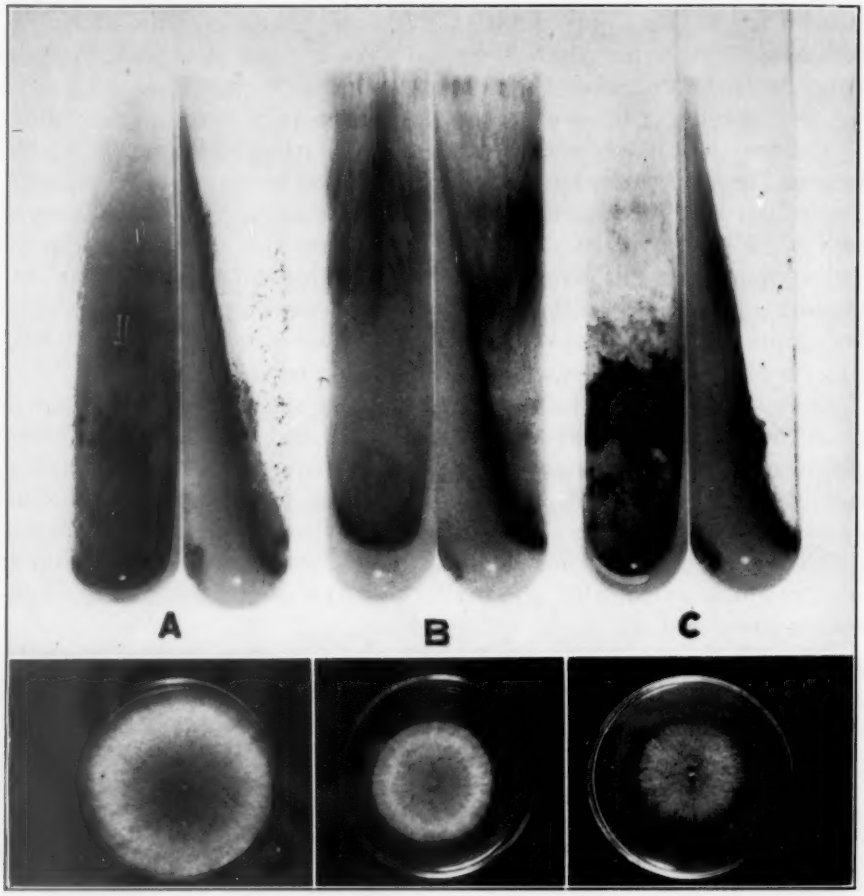

FIG. 1. Representative isolates of the three culture types of *Corticium solani*. Type A on the left, B in center, and C on the right. Above: Top and side views of the isolates grown for 2 weeks on potato-dextrose agar slants. Note differences in aerial growth and sclerotial production. Below: Diameter growth of the isolates after 48 hours at optimum temperatures.

24–25 can be combined in one group with an optimum temperature of 28° C. and with a 48-hour growth of from 30 to 60 sq. cm. Isolates 24–7 and 24–9 are respectively the slowest and most rapidly growing isolates of this group. Other isolates of this group, when growth area was plotted, fell between 40 and 60 sq. cm. The isolates comprising this group are of the cultural type A (Table 1). Isolates 24–3 and 24–26 represent culture type B, and

have an optimum temperature of 28–29° C. and a range of growth at 48 hours of 10 to 20 sq. cm. Isolates 24–62 and 24–28 represent culture type C, and their optimum temperature was from 24° to 26° C. and their maximum temperature was 33° C. as compared to a maximum of 40° C. for the other groups. Rarely did an isolate from one group fall within the growth limits of another, so that growth rate character could be used in conjunction with other growth characters in classifying an isolate.

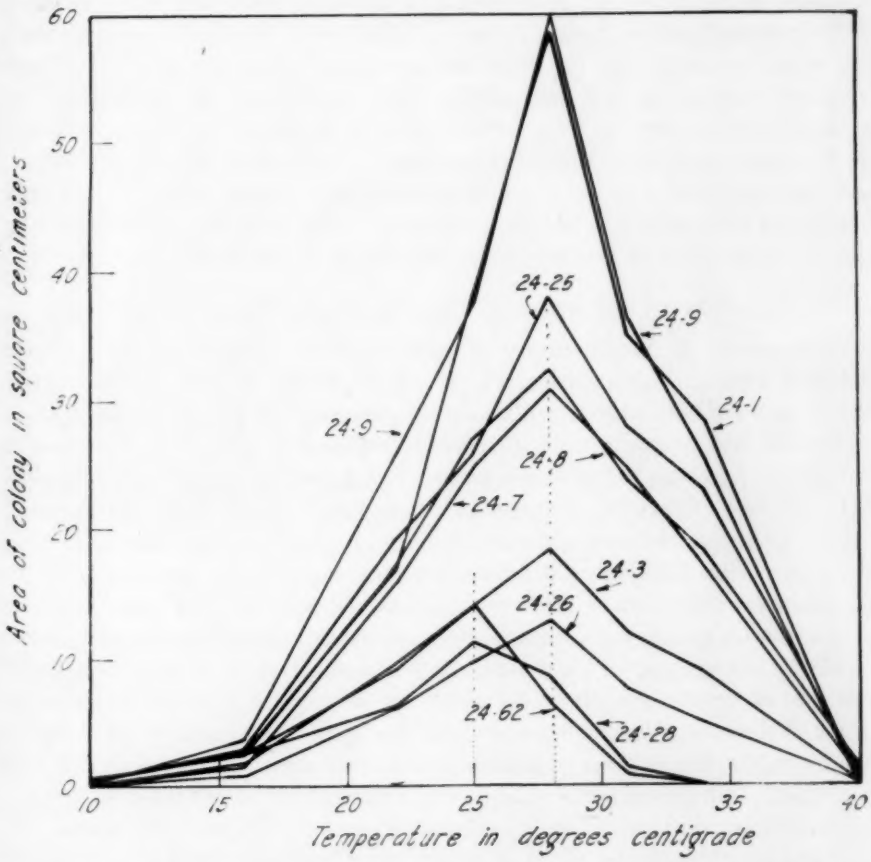

FIG. 2. The average growth on potato-dextrose agar of nine isolates of *Corticium solani* after 48 hours at nine different temperatures. Isolates 24–1, 24–7, 24–8, 24–9, and 24–25 are of culture type A; 24–3 and 24–26, culture type B; 24–28 and 24–62, culture type C. Types A and B have the same optimum and maximum temperatures but vary in rate of growth. Type C is distinct in that its optimum and maximum temperatures are below those of the other groups.

These results generally agree with previous work that has been done on different isolates of this fungus. Matsumoto (20) found the optimum temperature to be about 24° C. Müller (22) reported a temperature range of 4.5° to 30.8° C. with an optimum at 24° C. for the *Hypochnus solani* that he investigated. For the isolates he tested, Le Clerg (19) reported the optimum temperature for the sugar-beet isolates as 25° to 30° C. and for the

potato isolates as 20° to 25° C., but the growth rates were very similar at optimum temperatures. In figure 2, the growth of isolates 24–3 from sugar beet was approximately the same as Le Clerg's average for his sugar-beet isolates and the growth of isolate 24–62 from potato was about the same as that for his potato isolates. Walker (36), in working with an isolate of *Rhizoctonia solani* from cotton, found that the optimum temperature for growth was between 27° and 29° C., with the maximum growth being about the same as that of isolate 24–1 (Fig. 2). Monteith and Dahl (21), working with grass and potato strains, found wide variation in growth rates between the potato isolates, with the optimum growth between 25° and 30° C. and in most cases nearer 25° than 30°. Their curves for the growth of the grass isolates are very similar to the curves in figure 2 for isolates 24–1 and 24–9, except that their isolates grew about equally well at 25° and 30° C., the flat topped growth curve being only slightly higher at 30° C. If they had had a trial at 27° or 28° C., the curve might have been very similar to the curve obtained in this study for isolates 24–1 and 24–9.

MATERIALS AND METHODS USED IN PATHOGENICITY STUDIES

Differences in pathogenicity of isolates of *Corticium solani* have been noted by a number of investigators (10, 12, 17, 18, 19, 23, 30). In this study the trials were limited to inoculations by isolates from previously mentioned important hosts upon alfalfa (*Medicago sativa* L.), pink bean (*Phaseolus vulgaris* L.), cotton (*Gossypium hirsutum* L.), potato (*Solanum tuberosum* L.), spinach (*Spinacia oleracea* L.), sugar beet (*Beta vulgaris* L.) and tomato (*Lycopersicum esculentum* Mill.). In all of the experiments, except those involving field inoculations on growing sugar beets, two-thirds cu. ft. of steam-sterilized soil in flats was infested by adding to it giant cultures of the isolates grown for approximately one month upon 30 g. by dry weight of sterile oat grains. This amounted to the addition of approximately 0.1 per cent of organic matter to the soil. A like amount of oat culture subsequently steam-sterilized was added to the check flats. After addition of the inoculum, the soil was moistened and stirred daily for 6 to 8 days before planting. All experiments were in duplicate and were repeated twice.

Isolations were made from the diseased plants in the infested soil in each case and over 99 per cent of all isolations were *Corticium solani*. All proved to be the same isolate that was used in the inoculation.

PATHOGENICITY ON SEEDLINGS OF FIVE CROP HOSTS

The results of the pathogenicity trials on the seedlings of alfalfa, cotton, spinach, sugar beet, and tomato are in table 2. The total percentage of disease was a summation of the percentage of post-emergence and pre-emergence damping-off. This summation seemed justifiable because the isolates differed only slightly in their pathogenicity to seedlings of different ages.

The isolates of type A are, in general, very pathogenic on seedlings of the five hosts regardless of the host from which they were originally isolated.

TABLE 2.—*The relative pathogenicity of isolates of the three culture types of Corticium solani on seedlings of five hosts*

No. and culture type of isolate	Source of isolate	Total percentage of disease[a]				
		Alfalfa	Cotton	Spinach	Sugar beet	Tomato
Type A						
24– 9	Bean, Lima	100	98	96	90	78
24–49	Bean, Mung	100	100	83	57	90
24–52	Bean, Pink	98	96	85	78	63
24–21	Cotton	26	12	20	26	0
24–22	do	100	90	78	84	57
24–29	do	84	89	73	57	0
24–30	do	14	42	29	52	0
24–32	do	92	82	82	81	16
24–18	Cowpea, Blackeye	100	97	89	94	28
24–86	do	100	100	83	70	70
24–82	Fenugreek	78	72	74	57	13
24–42	Potato	100	89	79	98	98
24–14	Rhubarb	100	91	74	100	50
24– 8	Spinach	54	62	13	35	8
24–85	Squash	100	82	86	88	94
24– 1	Sugar beet	100	94	54	98	98
24–15	do	100	74	50	96	100
24–35	do	99	82	68	92	95
24–38	do	95	73	77	97	34
24–43	do	84	77	59	74	70
24–48	do	100	100	72	82	65
24–80	do	96	93	72	95	46
24–81	do	100	66	41	76	79
24–11	do	2	0	0	1	0
24– 7	Tomato	88	100	100	96	98
24–83	do	14	100	23	21	26
	Average	82	79	64	73	53
Type B						
24– 3	Sugar beet	0	0	0	16	0
24–17	do	31	0	0	0	0
24–24	do	14	11	0	1	10
24–27	do	1	0	0	1	0
24–34	do	1	0	8	0	0
24–36	do	1	0	0	2	0
24–37	do	39	1	0	3	0
24–40	do	0	0	0	13	19
24–45	do	0	22	0	28	0
	Average	10	4	1	7	3
Type C						
24–84	Alfalfa	27	5	16	0	0
24–76	Bean, Pink	5	0	10	0	0
35– 4	Celery	0	17	0	0	16
24– 4	Potato	14	12	0	0	0
24–13	do	9	0	13	28	0
24–19	do	2	0	4	0	0
24–28	do	1	0	0	25	0
24–51	do	19	13	15	11	0
24–69	do	2	12	0	0	0
35– 2	do	2	0	0	19	0
24– 6	Strawberry	1	0	3	0	0
35– 1	Tomato	9	0	0	10	2
35– 7	do	0	2	0	0	14
	Average	7	5	5	7	2
Control	Sterile soil	0	0	0	0	0

[a] The total percentage of disease was based upon the surviving stand of seedlings in the inoculated flats as compared to the control flats 20 days after planting.

There were a few isolates, particularly 24–21 and 24–30 from cotton and 24–8 from spinach, which were only moderately pathogenic. Isolates 24–11 and 35–11 from sugar beet caused little damping-off of any of the hosts. Isolate 24–11 was originally isolated from a sugar-beet seedling and 35–11 is closely related to it in that it was obtained from the resultant growth of a group of basidiospores dropped onto agar from the hymenium of 24–11. Isolates of type A were commonly found in nature infecting sugar beet, bean, cowpea, cotton, and spinach. Occasionally they were obtained from potato stem lesions.

The isolates of type B, in contrast to those of type A, have only slight seedling pathogenicity, occasionally being pathogenic to seedlings of one host but not to those of another. This might be expected of this group since isolates of this kind were not found on seedlings, and the writer has never isolated one of this type from natural infections on any host other than sugar beet.

Isolates of type C proved to be somewhat more pathogenic than those of type B, but at the most they were only slightly pathogenic on seedlings. They were commonly found infecting potato, producing sclerotia on tubers and lesions on stems and stolons. Very seldom have they been isolated from naturally infected seedlings of the hosts studied. Most isolates obtained from the naturally occurring basidiospore stage have been of this type.

In general, isolates of type A are capable of attacking the seedlings of all the hosts studied, whereas, those of type B are relatively nonpathogenic, and those of type C are somewhat variable in their degree of pathogenicity but are not severely pathogenic on seedlings. On alfalfa the average percentage of damping-off produced by all of the isolates comprising each of the three culture groups A, B, and C was 82, 10, and 7 respectively. The disease produced on the other hosts by the three culture types was approximately in this same ratio.

The susceptibility of the five hosts varied somewhat in that tomato was usually more resistant to attack than were any of the others. This was especially true of those isolates with only a moderate degree of pathogenicity. Spinach was somewhat more resistant than alfalfa, cotton, or sugar beet, and alfalfa was generally the most susceptible.

There was no damping-off of the seedlings in any of the control flats of steam sterilized soil.

PATHOGENICITY ON PINK BEAN

Rhizoctonia lesions on bean plants in the field may be observed at almost any stage of growth. The surface scabbing of the older stems, however, is apparently a result of a partial healing and recovery from an earlier infection. The first record of Rhizoctonia injury to bean seedlings was given by Atkinson (1). He reported that the fungus caused damping-off of bean seedlings and attacked plants that were 6 to 10 inches high. In 1901 Duggar and Stewart (10) reported this fungus as the cause of a stem rot of red kidney beans in the field. Since that time there have been many reports on its occurrence on beans.

TABLE 3.—*The relative pathogenicity of isolates of the three culture types of Corticium solani on pink bean*

No. and culture type of isolate	Source of isolate	Emergence	Diseased seedlings	Injury rating[a]	Points of injury listed in order of importance
		Per cent	*Per cent*		
Type A					
24– 9	Bean, Lima	28	100	3	Primary root, hypocotyl
24–49	Bean, Mung	58	98	3	do
24–52	Bean, Pink	60	88	3	do
24–21	Cotton	96	0	0	Scabbing on surface
24–22	do	38	100	3	Primary root, hypocotyl
24–29	do	98	100	3	do
24–30	do	100	70	2	Hypocotyl
24–32	do	84	100	3	Primary root, hypocotyl
24–18	Cowpea, Blackeye	44	92	3	do
24–86	do	78	91	3	do
24–82	Fenugreek	64	82	2	Hypocotyl
24–42	Potato	18	100	3	Primary root, hypocotyl
24–14	Rhubarb	22	100	3	do
24– 8	Spinach	92	0	0	Scabbing on surface
24–85	Squash	56	100	3	Primary root, hypocotyl
24– 1	Sugar beet	16	100	3	do
24–15	do	46	100	3	do
24–35	do	74	100	3	do
24–38	do	80	100	3	do
24–43	do	80	98	3	Hypocotyl, primary root
24–48	do	94	100	3	do
24–80	do	88	100	3	do
24–81	do	34	100	3	Primary root, hypocotyl
24–11	do	84	8	1	Hypocotyl
24– 7	Tomato	26	100	3	Primary root, hypocotyl
24–83	do	20	100	3	do
	Average	61	86	2.6	
Type B					
24– 3	Sugar beet	98	10	1	Hypocotyl
24–17	do	96	0	0	No injury
24–24	do	94	5	1	Hypocotyl
24–27	do	98	0	0	No injury
24–34	do	98	60	1	Hypocotyl
24–36	do	98	0	0	No injury
24–37	do	98	60	1	Hypocotyl
24–40	do	98	0	0	No injury
24–45	do	98	18	1	Hypocotyl
	Average	97	17	0.6	
Type C					
24–84	Alfalfa	98	0	0	No injury
24–76	Bean, Pink	98	0	0	do
35– 4	Celery	96	10	1	Hypocotyl
24– 4	Potato	100	0	0	No injury
24–13	do	96	0	0	do
24–19	do	62	60	2	Hypocotyl
24–28	do	100	0	0	No injury
24–51	do	92	0	1	Hypocotyl
24–69	do	96	0	0	No injury
35– 2	do	98	0	0	do
24– 6	Strawberry	100	0	0	do
35– 1	Tomato	100	0	0	do
35– 7	do	97	0	0	do
	Average	95	5	0.3	
Control, sterile soil		100	0	0	No injury

[a] 0 = healthy; 1 = slightly diseased; 2 = moderately diseased; 3 = severely diseased or dead.

In this study certain isolates were capable of attacking the primary root of the young plant both before and after emergence of the cotyledons. This attack was usually associated with swelling and distortion of the hypocotyl and with hypocotyl lesions. Other isolates caused no injury to the primary root, but severely injured the hypocotyl. Others produced no injury whatever. Since the infections varied as to their degree of severity, an injury

FIG. 3. The common types of lesion on pink-bean seedlings produced by isolates of *Corticium solani*. The large seedling on the left has typical hypocotyl lesions commonly produced by isolates of type A or occasionally B. The smaller seedlings on the right have the primary root, hypocotyl, cotyledon, and leaf lesions of the type often produced by isolates of type A. The seedlings were the same age when photographed, but the two on the right were greatly stunted because of the more severe injury.

rating of 0 for healthy to 3 for severely diseased was used in the classification of the diseased plants and as a means of rating the pathogenicity of the isolates. The rating was based upon the percentage emergence and the degree of injury to each plant at the end of four weeks. This seemed to be a somewhat more accurate measure of the pathogenicity than the percentage of disease alone. The results obtained from the inoculations on pink bean are summarized in table 3.

Isolates of type A with but few exceptions were strongly pathogenic on pink bean, in some cases causing severe pre-emergence injury to the primary root and hypocotyl. These few that produced slight injury were the same isolates that proved to be weakly pathogenic in the seedling trials. The isolates obtained from naturally infected beans and related hosts were predominately type A, so this group might be expected to be very pathogenic to beans.

Here again, the isolates of the culture types A and B can be separated on the basis of their ability to produce disease. Although some B isolates caused small hypocotyl lesions, none of them were strongly pathogenic and none produced pre-emergence injury or injury to the primary root (Fig. 3). Thus, the most pathogenic isolates of this group were given an injury rating of only 1 as compared to a rating of 3 for the majority of those in group A. Isolates of type B have never been obtained from naturally infected beans.

Isolates of type C were variable in their pathogenicity on beans but with only two isolates, 24–19 from potato and 24–83 from tomato, was there severe injury to the plants. It is of interest that isolate 24–52 originally obtained from a very small hypocotyl lesion on pink bean was non-pathogenic. Occasionally isolates of this type were obtained from naturally infected beans, but seldom did they produce appreciable injury either to the plant from which isolated or to reinoculated plants.

The average percentage of diseased seedlings produced by all individuals of each of the culture groups A, B, and C was 86, 17, and 5, respectively, with corresponding degrees of injury of 2.6, 0.6, and 0.3.

PATHOGENICITY ON POTATO

The attack of *Corticium solani,* then known as *Rhizoctonia solani,* on potato has been known in Europe since 1858 when Kühn (15) described the disease and named the fungus. In the United States Duggar and Stewart (10) first reported the Rhizoctonia disease of potato from New York in 1901. Differences in pathogenicity of potato isolates have been noted by Dana (6), Drayton (7), Duggar (9), Gussow (14), Le Clerg (18, 19), Rolfs (30), Rosenbaum and Shapovalov (31), Sanford (33), and others.

For inoculation tests, seed tubers of the White Rose variety free from Corticium sclerotia were surface sterilized with a 1 to 1000 solution of bichloride of mercury for 1½ hours and planted in soil infested with the isolates. For each isolate a total of thirty tuber pieces each containing a single eye were used in a series of three replications.

The plants were grown for two months after which they were removed and the stems examined for lesions and sclerotia. The results of these trials are presented in table 4.

Most of the isolates of group A were pathogenic on the stems and stolons of potato but produced relatively few sclerotia on the tubers. A large majority of the stem lesions resulting from the attack by type A were more severe than those produced by the other two types and often resulted in

complete girdling at the point of infection (Fig. 4). The bean, potato, tomato, and sugar-beet isolates of type A were strongly pathogenic causing a high percentage of infection. The cotton and spinach isolates were somewhat less pathogenic. The isolates 24–30 from cotton and 24–8 from spinach produced no infections on the stems or stolons.

TABLE 4.—*The relative pathogenicity and sclerotial production of isolates of the three culture types of Corticium solani on potato*

No. and culture type of isolate	Source of isolate	Shoots emerged from 30 tuber pieces	Diseased shoots	Sclerotial production	Degree of injury[a]
		Number	*Per cent*		
Type A					
24– 9	Bean, Lima	30	100	+	3
24–52	Bean, Pink	24	68	+	2
24–21	Cotton	25	10	0	1
24–22	do	26	6	0	1
24–30	do	26	0	0	0
24–18	Cowpea, Blackeye	22	60	0	2
24–42	Potato	20	61	+	3
24– 8	Spinach	32	0	0	0
24– 1	Sugar beet	30	50	0	2
24–15	do	18	33	0	2
24–25	do	20	40	+	2
24–11	do	24	16	0	1
24– 7	Tomato	34	100	+	3
	Average	25	42		1.7
Type B					
24– 3	Sugar beet	28	0	0	0
24–17	do	22	10	0	1
24–24	do	24	0	0	0
24–26	do	28	0	0	0
24–27	do	24	0	0	0
	Average	25	2		0.2
Type C					
24– 4	Potato	21	18	++	1
24–13	do	22	40	++	2
24–19	do	20	10	+	1
24–28	do	24	4	++	1
24–51	do	26	10	++	1
24–69	do	24	12	++	1
35– 2	do	26	8	+++	1
35– 7	Tomato	30	3	+	0
	Average	24	13		1.0
Control		30	0	0	0

[a] 0 = healthy; 1 = slightly diseased; 2 = moderately diseased; 3 = severely diseased with no chance of continued growth, or dead.

Isolates of type B from sugar beets in contrast to those of type A from the same host were weakly pathogenic. Only one isolate, 24–17, produced any infection, and this was mostly superficial causing no great injury to the stem. No sclerotia were produced on the tubers or stems by any type B isolate.

In nature the potato is the most common host for isolates of type C (Table 1). In the inoculation trials the isolates of this type were variable

in regard to their pathogenicity on potato but all produced some disease. The fact that this type produces large numbers of sclerotia on the stems and tubers (Fig. 4) undoubtedly explains the widespread distribution and constant association of this type with potato.

These results show that the isolates that are most pathogenic to seedlings, namely those of the A type, were also the most destructive to potato plants. The fact that the potato isolates of the C type produced more disease on potato than on the other hosts studied indicates a degree of host specialization for the group.

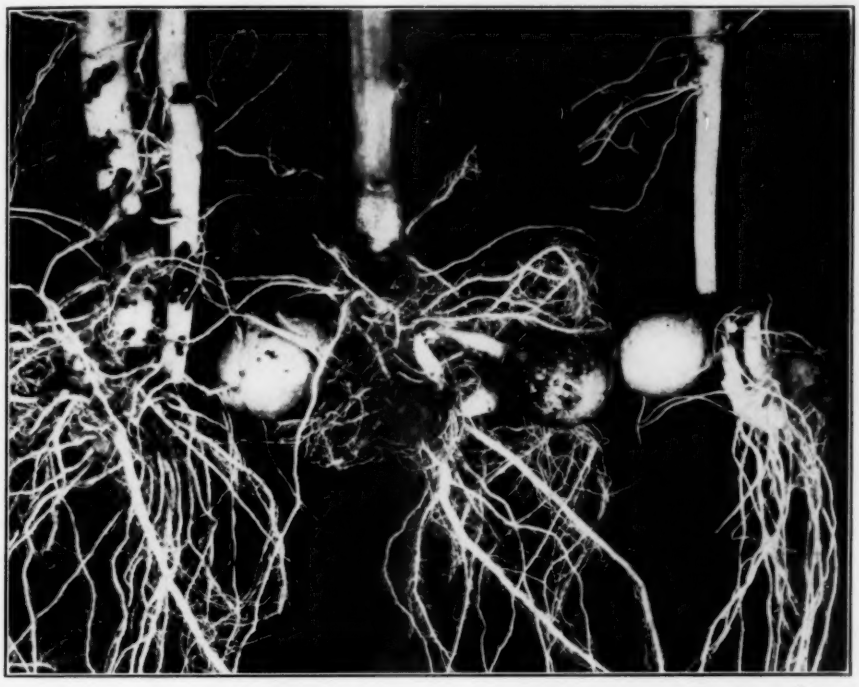

FIG. 4. The two potato plants on the left have the abundant sclerotia commonly produced by isolates of culture type C on the stems and tubers. Stem cankers were occasionally produced by this type. The plant on the right shows the typical stem girdling produced by isolates of type A. Two stems have broken off at the lesion.

PATHOGENICITY ON SUGAR-BEET ROOTS

The rotting of sugar-beet roots by *Corticium solani* after the plants are beyond the seedling state is of common occurrence and has been known for many years. Pammel (23) in 1891 described Rhizoctonia rot of sugar beets and named the fungus *Rhizoctonia betae* Kühn. Duggar (8) reported the occurrence of Rhizoctonia on sugar beets in America in 1899. In 1915 Edson (11) reported that *R. solani* was capable of attacking the sugar beet at any age without the presence of wounds. Edson and Shapovalov (12) reported a number of isolates of *R. solani* from sugar beet as being able to attack potato. Le Clerg (16) showed that sugar-beet isolates were patho-

genic on sugar-beet roots and seedlings while potato isolates were not. Later (17, 18, 19), he found that some isolates from potato were able to attack sugar beets. Peltier (24) found a sugar-beet isolate pathogenic to carnations. Wiant (38) tested two isolates from sugar beets and found them pathogenic on conifer seedlings, peas, cabbage, eggplant, pepper, and tomato.

This fungus is the cause of dry-rot canker, in certain regions the most important root rot of the sugar beet. The infection may be rather general over an entire field or limited to small circular areas where nearly 100 per cent of the plants may be killed during the season. The symptoms on the parts below ground may be of two types (Fig. 5). The more common type

FIG. 5. The common symptoms produced by *Corticium solani* on sugar beets. On the left is the sunken concentric-ringed dry-rot canker. The beet on the right shows a sectional view of the crown-rotting phase.

is the more or less localized lesions of dry shrunken tissue each with concentric rings of lighter and darker brown dead tissue and with the internal tissue converted into a dry spongy mass in a definite pocket sharply delimited from the healthy tissue. Occasionally a large open canker is produced in which the dry diseased tissue cracks open widely, probably because of the continued increase in the circumference of the unaffected portion of the root. The other type is the crown infection resulting in the complete destruction of the crown tissues and the death of the leaves. Both kinds of infection may be produced by the same isolate.

During two seasons sugar beets growing in a field that was apparently free from natural infection were inoculated with 26 isolates of this fungus from various hosts. The fungus was grown on sterilized oats as previously

described and when the beets in the field were from 1½ to 3 inches in diameter, each was inoculated with 8 to 10 infested oat grains. The inoculum was placed in contact with or very near the uninjured root or sprinkled between the petioles of the leaves on the crown of the plant. In three randomized replications a total of 45 root and 45 crown inoculations were made with each isolate. During the growing season counts were made at monthly intervals and all dead beets staked so that they could be accounted for at the end of the season. The roots were dug after approximately five months at which time they were segregated into five classes, 0 to 4 (Fig. 6), as determined by the degree of injury. From a practical standpoint isolates pro-

FIG. 6. Sugar beets infected by *Corticium solani* following inoculation by placing the inoculum at the side of the injured roots. Examples of the four degrees of infection (1 to 4) used in the classification of diseased roots.

ducing an average injury rating of less than 0.8 can be considered as non-injurious.

Plants with previously injured roots were inoculated with several isolates, and with pathogenic isolates these plants died sooner than plants with uninjured roots. In no case did the isolates which failed to infect sound roots produce any disease other than a scabbing on the surface of the roots that were wounded. In such cases the wound healed very rapidly.

The results of the inoculation trials on sugar beets are in table 5. In the root inoculations, isolates of type A produced a high percentage of disease with the exception of the cotton isolate 24–21 which was mildly parasitic in these trials. In most cases the injury was severe, often resulting in the death of many of the plants within a month after inoculation. Eight of the eleven isolates produced over 95 per cent disease with corresponding degrees of injury greater than 2.9. This indicates the extreme virulence of

culture type A. Isolate 24–11, originally isolated from a sugar-beet seedling, was only moderately pathogenic on the older roots as compared with the other sugar beet isolates. The type A isolates that produced a high percentage of disease on the roots were also capable of invading the crown tissues. However, there was usually somewhat less infection produced by crown inoculation. The percentage of infection and degree of injury produced by isolates 24–29 and 24–11 were markedly low in the crown inoculations.

Isolates of type B also proved to be extremely pathogenic on sugar beet roots. The six isolates tested produced an average disease percentage of 97 and an injury rating of 3.0. Each isolate produced greater than 87 per cent disease. This virulence was outstanding as a point of distinction for these

TABLE 5.—*The relative pathogenicity of isolates of the three culture types of Corticium solani on sugar beet roots and crowns*

No. and culture type of isolate	Source of isolate	Root inoculations		Crown inoculations	
		Average degree of injury[a]	Disease, per cent	Average degree of injury[a]	Disease, per cent
Type A					
24– 9	Bean, Lima	3.4	100	3.5	100
24–52	Bean, Pink	2.2	82	2.2	76
24–21	Cotton	0.3	18	0.0	0
24–29	do	2.9	96	0.1	2
24–18	Cowpea, Blackeye	3.0	98	1.9	62
24–42	Potato	3.5	100	3.1	93
24–14	Rhubarb	3.6	100	2.9	93
24– 1	Sugar beet	3.6	100	3.5	100
24–15	do	3.5	100	2.8	93
24–25	do	3.0	98	2.3	82
24–11	do	1.2	47	0.3	11
	Average of group	2.7	85	2.1	65
Type B					
24– 3	Sugar beet	2.8	100	0.4	16
24– 5	do	2.5	93	0.2	9
24–17	do	2.4	87	0.6	20
24–24	do	3.2	100	0.3	13
24–26	do	3.1	100	0.4	16
24–27	do	3.7	100	0.8	29
	Average of group	3.0	97	0.5	17
Type C					
24–12	Asparagus	0.9	29	0.0	0
24–76	Bean, Pink	0.1	4	0.2	7
24–13	Potato	0.3	13	0.0	0
24–19	do	0.8	24	0.1	2
24–51	do	0.5	22	0.1	2
24–64	do	0.2	11	0.3	11
35– 2	do	0.6	22	0.1	2
24– 6	Strawberry	0.6	22	0.3	11
24–10	Tomato	0.6	22	0.1	2
	Average of group	0.5	19	0.1	4
Control		0.0	0	0.0	0

[a] 0 = healthy; 1 = slight infection; 2 = moderate infection; 3 = moderate–severe infection; 4 = severe infection.

isolates because of the fact that they were, from a practical standpoint, nonpathogenic on seedlings, including those of sugar beet. Also, when inoculated on the crown of the beet, isolates of this type were unable to infect the petioles and crown tissues, thus differing from most isolates of type A in this respect. Undoubtedly these are the reasons for the writer's failure to find isolates of type B commonly associated with natural seedling or sugar-beet crown infections. All of these isolates were obtained from the dry-rot canker stage of the disease on the sugar-beet roots.

The relatively low incidence of disease resulting from either crown or root inoculations with type C isolates sets them off as a distinct group differing from the other two groups in their ability to infect sugar beet. Since this type is that commonly associated with the black scurf disease of potato, these results agree with those of Le Clerg (16, 18) who found that most of the potato isolates were relatively nonpathogenic on sugar beet although an occasional isolate from potato stolons was able to readily infect sugar-beet roots. The type A potato isolate 24–42 was of this latter type and in these trials proved to be extremely pathogenic on sugar beets resulting in infections of 100 and 93 per cent in the root and crown inoculations, respectively.

DISCUSSION

The results of the pathogenicity trials clearly indicate that the fungus *Corticium solani* can readily be separated into pathogenically as well as culturally different strains. Some of these strains are limited in their attack to a certain host plant and over a period of years have been found constantly associated with this plant. Others, however, are capable of attacking a wide variety of plants and cannot be considered as being specific to any one particular host. In these trials the strain designated as type A was obtained from many hosts and is clearly a polyphagous strain showing no host specificity, whereas the strains designated as types B and C are highly specific as to hosts. The isolates of type B were obtained only from sugar beet roots, and those of type C were largely from potato and from basidiospores produced in nature.

Although type B occasionally produced some disease on hosts other than sugar beet in the inoculation trials, it has not as yet been found attacking any host other than this in nature. Besides being limited in pathogenicity to this one host, this strain invades only the enlarged root since it apparently cannot infect through the crown tissues nor is it pathogenic on sugar beet seedlings. Isolations from naturally infected beet roots have shown that isolates of group B are recovered only from infections originating below the crown.

Isolates of type C were obtained largely from potato and were somewhat variable in their ability to produce disease. They had little effect upon the seedlings of the hosts tested but showed a moderate degree of pathogenicity on potatoes. This was particularly true of those originally isolated from potato stem lesions or sclerotia. In general, isolates of this type compared

with those of type A must be classified as very slightly pathogenic on all hosts other than potato.

The variation in pathogenicity is much greater when the isolates are grouped according to their original host than when grouped on the basis of culture type. Consequently, the culture type is often of more importance than is the host from which isolated when attempting a prediction of the possible pathogenicity and host range of an isolate. Because of this fact the generalization that all isolates from one host will or will not be pathogenic on another cannot be made. The fallacy of such a generalization is emphasized when a comparison of the pathogenicity of all the sugar-beet isolates is made. Such a group comprises isolates of A and B culture types both of which commonly affected sugar-beet roots and proved to be equally virulent when reinoculated onto the roots, but differed markedly in their ability to infect other hosts. Since both A and C isolates can attack potato and have been obtained from this host, it cannot be said in a general sense that potato isolates are nonpathogenic on hosts such as bean or sugar beet.

These results indicate that the cultural characteristics of an isolate of *Corticium solani* are more important in the prediction of the host specificity or lack of specificity of that isolate than is the host plant from which it was isolated. This is an important consideration in any area where a polyphagous strain occurs.

SUMMARY

From 260 isolations of *Corticium solani* from 15 different crop plants, 52 isolates were selected for pathogenicity studies. The selections were made on the basis of cultural characters and observed pathogenicity.

The isolates were separated into three culture types designated as A, B, and C based upon the following cultural characters: thickness and coloration of the stroma-like layer on the surface of the medium; size, abundance, and color of the sclerotia; abundance and color of the aerial mycelium; darkening of the agar medium; and growth rate. Isolates in group B were obtained only from sugar-beet roots in the field.

The effect of temperature upon the growth of 25 isolates was tested. The results were similar to those obtained for *Corticium solani* by other investigators. The majority of isolates had an optimum temperature of 28° C. and a maximum temperature of 42° C., and were variable in their rate of growth. The isolates of type C differed from this in that they had an optimum temperature of 25° C. and a maximum temperature of 33° C. This difference clearly sets this group off as a distinct temperature group. There was some overlapping of growth rates among the three groups so this method of separating them could be used only in conjunction with the other cultural characters.

The pathogenicity of 52 isolates was tested on alfalfa, cotton, pink bean, potato, spinach, sugar beet, and tomato.

Alfalfa seedlings proved to be susceptible to the attack of many of the isolates. In general type A was highly pathogenic to alfalfa, whereas B

and C were variable in virulence, but in no case highly pathogenic. The basidiospore isolates of type C were only slightly pathogenic. This is also true of isolate 24–11 of type A, which under certain conditions produced basidiospores on the inoculated host plants.

Cotton was susceptible to the same isolates that attacked alfalfa. The isolates of type A were the most destructive. Those of type B were practically nonpathogenic and those of type C were variable in pathogenicity.

Spinach seedlings were less susceptible than alfalfa or cotton. However, isolate 24–7 of type A was very destructive. The isolates of type A were moderately to severely pathogenic, those of type B were nonpathogenic, and those of type C were variable in their degree of pathogenicity but in no case were they severely pathogenic.

Tomato seedlings were killed by this fungus primarily in the pre-emergence stage. Isolates of type A were more variable in their attack on this host than on the others. Isolates of types B and C were nonpathogenic or only slightly pathogenic.

Sugar-beet seedlings were very susceptible to isolates of type A and to certain ones of type C. Others of type C and those of type B were only slightly pathogenic.

On pink beans, as on other hosts, the isolates of type A were very destructive. The isolates of types B and C were slightly pathogenic and produced symptoms on the beans which were different than those produced by the more pathogenic isolates.

The isolates of type A produced severe cankers on potato stems but only few sclerotia on the tubers. Isolates of type B produced no cankers or sclerotia, whereas those of type C produced a moderate number of cankers and many sclerotia.

Isolates of type A were able to infect growing sugar beet roots either through the crown or root, whereas isolates of type B could infect only through the root. This latter group could not infect sugar beet or other seedlings to any extent and is apparently a specialized group able to infect only the growing root of the sugar beet.

Prediction of the possible pathogenicity of any isolate of *Corticium solani* obtained from the more important host plants in California is more accurate when based upon the known pathogenicity of the culture type to which it belongs than when based upon the host from which it was isolated. Two isolates of different culture types having the same degree of pathogenicity on one host are not necessarily equally virulent in their attack upon another host.

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SPECIALIZATION IN ERYSIPHE GRAMINIS FOR PATHOGENICITY ON WILD AND CULTIVATED GRASSES OUTSIDE THE TRIBE HORDEAE[1]

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In previous papers (1, 2) it has been reported that most of the specialized races of *Erysiphe graminis* DC. studied from grasses in the tribe Hordeae and the genus *Poa* are not restricted in infection to the species of any one genus. This paper describes the pathogenicity of cultures from other grasses.

LITERATURE REVIEW

A general review of the literature dealing with host specialization in *Erysiphe graminis* and a detailed review of previous results with the fungus on grasses in the tribe Hordeae and the genus *Poa* have been presented (1, 2). Therefore, this review is restricted to the literature concerned with fungus cultures studied from other grasses.

The specialized variety, *Erysiphe graminis avenae*, as distinguished by Marchal (5) infected *Avena fatua*, *A. orientalis*, *A. sativa*, and *Arrhenatherum elatius* but not *Hordeum vulgare*, *Secale cereale*, or *Triticum vulgare*. Likewise, he implied that there was no infection on species of *Agropyron*, *Bromus*, or *Poa*.

Salmon (8) reported that conidia from *Avena sativa* infected *A. brevis*, *A. nuda*, *A. orientalis*, *A. sativa*, *A. sterilis*, and *A. strigosa*, but not *Arrhenatherum elatius*, *Alopecurus pratensis*, *Dactylis glomerata*, *Festuca elatior*, *F. heterophylla*, *Hordeum vulgare*, *Lolium italicum*, *Phleum pratense*, *Poa annua*, *Secale cereale*, *Trisetum pratense*, or *Triticum vulgare*. Conidia from *Avena nuda* infected *A. brevis*, *A. nuda*, and *A. sativa*. In addition, Salmon (10) states that conidia from *Avena sterilis* produced full infection on *A. sativa*, subinfection on *A. pratensis* and on one leaf of *Arrhenatherum avenaceum*, but no infection on *Bromus sterilis*, *B. unioloides*, *Festuca elatior*, or *Lolium temulentum*.

Reed (7) found that conidia from *Avena sativa* infected *Avena barbata* Pott, *A. brevis* Roth, *A. chinensis* Fisch., *A. fatua* L., *A. fatua* L. var. *glabrata*, *A. ludoviciana* Dur., *A. nuda* L., *A. nuda* L. var. *elegantissima*, *A. orientalis* Schreb., *A. planiculmis* Schrad., *A. pratensis* L., *A. pubescens* Huds., *A. purpurea* Gueldenst, *A. sativa* L., *A. sterilis* L., *A. strigosa* Schreb., *A. sulcata* F. Gay, and *Arrhenatherum avenaceum* Beauv.; but there was no infection of *Avena bromoides* Gouan, *A. sempervirens* Vill..

[1] The investigation reported in this paper is in connection with a project of the Kentucky Agricultural Experiment Station and is published by permission of the director. The study was begun by the author at the University of Michigan.

[2] The writer acknowledges with gratitude the suggestions and criticisms given by Dr. E. B. Mains, seed of grasses supplied by many collaborators, cultures of the fungus sent by Dr. George W. Fischer, and the assistance of Mr. J. R. Swallen in checking the identity of the majority of the grasses used.

Holcus lanatus L., *Hordeum vulgare* L., or *Triticum vulgare* Vill. Reed (6) reported that oat mildew infected a small percentage of seedlings of *Arrhenatherum elatius.*

Erysiphe graminis bromi was distinguished by Marchal (5) as occurring on different species of *Bromus,* notably *B. mollis* and *B. sterilis.* Conidia from these two species would not infect *Hordeum vulgare.* Furthermore, this specialized variety would not infect species of *Agropyron* or *Poa, Avena sativa, Secale cereale,* or *Triticum vulgare.*

Salmon (8, 9) reported results of an extensive study of *Erysiphe graminis bromi.* His work indicates the occurrence of at least five specialized races, one on each of the following: *Bromus arvensis, B. commutatus, B. hordeaceus* var. *glabrescens, B. interruptus,* and *B. tectorum.*

Marchal (5) found that *Erysiphe graminis* from *Holcus lanatus* and *Festuca pratensis* would not infect *Hordeum vulgare,* but reactions of other grasses are not given.

Salmon (10) reported that *Erysiphe graminis* from *Dactylis glomerata* infected *D. glomerata* but not *Agropyron repens, Avena sativa, Hordeum vulgare, Lolium temulentum, Secale cereale,* or *Triticum vulgare.*

MATERIALS AND METHODS

Selected groups of accessions of 123 species and 8 varieties in 28 genera listed in table 1 were tested with 8 cultures of *Erysiphe graminis* obtained from grasses outside the tribe Hordeae. The methods of handling fungus cultures and grasses and of making inoculations have been fully described (1). The classes of reactions, 0 to 4, used in recording notes were those of Mains and Dietz (4, p. 231).

The term "grass accession" has been explained, as well as the precautions taken to assure accuracy in regard to the specific identity of the grasses used in all experiments (2, p. 65–66).

RESULTS

In table 1 are the general results of inoculating from 1 to many accessions of 123 species and 8 varieties of grasses with 8 cultures of *Erysiphe graminis* from 7 genera. These results demonstrate that powdery mildew is not necessarily restricted to the species of the source genus. The large-scale negative evidence permits a better understanding of the host range of additional isolates of *E. graminis.* The grass accessions listed as infected in table 1 include all cases where definite infection was recorded.

Distinction between resistant and susceptible types of reaction of grass accessions is made in table 2. The 39 accessions of various grass species listed in table 2 were selected because of their significance in illustrating the differences in pathogenicity as well as the extent of the host range of the 8 cultures.

Culture 5. On Avena sativa, from Ann Arbor, Michigan

Of the many grass species tested culture 5 infected only *Avena sativa* and *Trisetum flavescens.* Infection of the latter furnishes further proof

TABLE 1.—*The number of accessions of various grass species infected after inoculation with 8 cultures of Erysiphe graminis from 7 genera of grasses*

Species tested[a]	Culture no. and source genus							
	Agrostis	*Avena*	*Avena*	*Polypogon*	*Dactylis*	*Bromus*	*Festuca*	*Koeleria*
	23	5	17	8	12	15	16	19
	Number of accessions infected[b]							
Aegilops crassa Boiss.	.....	0/1	0/1	0/1	0/1	0/2	0/1	.....
A. cylindrica Host	0/1	.....	0/1	0/1	0/1	0/1	0/1	.....
A. triuncialis L.	.....	0/1	.....	.....	.....	.....	.....	.....
Agropyron caninum (L.) Beauv.	0/1	.....	.....	.....	.....	.....	.....	.....
A. cristatum (L.) Beauv.	0/1	0/4	0/4	0/4	0/4	0/4	0/4	0/1
A. desertorum (Fisch.) Schult.	0/1	0/1	0/1	0/1	0/1	0/1	0/1	0/1
A. inerme (Scribn. and Smith) Rdyb.	.....	0/12	0/11	0/11	0/11	0/11	0/11	0/3
A. intermedium (Host) Beauv.	.....	0/1	.....	.....	.....	.....	.....	0/1
A. repens (L.) Beauv.	0/1	0/1	.....	.....	.....	.....	.....	0/1
A. semicostatum (Steud.) Nees	.....	0/1	0/1	0/1	0/1	0/1	0/1	0/1
A. sibiricum (Willd.) Beauv.	.....	0/5	0/5	0/5	0/4	0/5	0/5	0/2
A. smithii Rydb.	.....	0/1	0/1	0/1	0/1	0/1	0/1	0/1
A. spicatum (Pursh) Scribn. and Smith	0/1	0/13	0/11	0/5	0/12	0/12	0/12	0/3
A. striatum (Steud.) Nees ex Hook.	.....	.....	0/1	0/1	0/1	0/1	0/1	.....
A. subsecundum (Link) Hitchc.	.....	0/1	0/1	0/1	0/1	0/1	0/1	.....
A. trachycaulum (Link) Malte	0/1	0/14	0/14	0/14	0/14	0/14	0/14	0/3
Agrostis alba L.	1/3	0/4	0/4	2/4	0/4	0/4	0/4	0/4
A. exarata Trin.	1/1	0/1	0/1	1/1	0/1	0/1	0/1	0/1
A. hiemalis (Walt.) B.S.P.	.....	.....	0/1	0/1	0/1	.....	0/1	.....
A. interrupta L.	.....	.....	0/1	1/1	0/1	0/1	0/1	.....
A. palustris Huds.	0/1	0/1	0/1	1/1	0/1	0/1	0/1	.....
A. scabra Willd.	.....	.....	.....	0/1	0/1	.....	1/1	.....
A. spica-venti L.	.....	.....	0/1	0/1	0/1	0/1	0/1	.....
A. stolonifera L.	.....	.....	0/1	1/1	0/1	0/1	0/1	.....
Alopecurus aequalis Sobol.	.....	.....	0/1	0/1	0/1	0/1	0/1	.....
A. pratensis L.	0/1	.....	0/3	2/3	0/3	0/3	0/3	0/1
Arrhenatherum elatius (L.) Mert. and Koch	0/1	0/1	1/1	1/1	0/1	0/1	0/1	0/1
Avena brevis Roth	.....	.....	1/1	.....	.....	.....	.....	.....
A. fatua L.	.....	.....	2/2	.....	0/1	0/1	0/1	.....
A. nuda L.	.....	.....	1/1	.....	.....	.....	.....	.....
A. orientalis Schreb.	.....	.....	1/1	.....	.....	.....	.....	.....
A. sativa L.	0/1	1/1	34/34	0/7	0/1	0/1	0/1	0/1
Beckmannia erucaeformis (L.) Host	0/1	0/1	0/1	1/1	0/1	0/1	0/1	0/1
B. syzigachne (Steud.) Fernald	1/1	0/1	0/1	1/1	0/1	0/1	0/1	0/1
Bromus arvensis L.	.....	0/2	0/2	0/2	0/2	0/2	0/2	.....
B. brizaeformis Fisch. and Mey.	.....	0/1	0/1	0/1	0/1	0/1	0/1	.....
B. carinatus Hook. and Arn.	0/2	.....	0/2	0/2	0/2	2/2	0/2	0/2
B. catharticus Vahl	0/1	0/3	0/3	0/3	0/2	1/3	0/3	.....
B. commutatus Schrad.	.....	0/1	0/1	0/1	0/1	0/1	0/1	.....
B. inermis Leyss.	.....	0/6	0/4	0/6	0/5	0/6	0/6	0/1
B. japonicus Thunb.	.....	0/2	0/2	0/2	0/2	0/2	0/2	.....
B. macrostachys L.	.....	0/2	0/2	0/2	0/2	0/2	0/2	.....
B. macrostachys var. *lanuginosus* Boiss.	.....	0/1	0/1	0/1	0/1	0/1	0/1	.....
B. marginatus Nees	.....	0/7	0/8	0/8	0/5	3/8	0/8	0/2
B. mollis L.	.....	0/2	0/2	0/2	0/2	0/2	0/2	.....
B. polyanthus Scribn.	.....	0/1	0/1	0/1	0/1	0/2	0/1	.....
B. purgans L.	.....	0/2	0/2	0/2	0/1	0/2	0/2	.....

TABLE 1.—(*Continued*)

Species tested[a]	Culture no. and source genus							
	Agrostis	*Avena*	*Avena*	*Polypogon*	*Dactylis*	*Bromus*	*Festuca*	*Koeleria*
	23	5	17	8	12	15	16	19
	Number of accessions infected[b]							
B. rigidus Roth	.....	0/1	0/1	0/1	0/1	0/1	0/1	.....
B. rubens L.	.....	0/1	0/1	0/1	0/1	0/1	0/1	.....
B. secalinus var. *velutinus* (Schrad.) Koch	.....	0/1	0/1	0/1	0/1	0/1	0/1	.....
B. squarrosus L.	.....	0/1	0/1	0/1	0/1	0/1	0/1	.....
B. tectorum L.	.....	0/1	0/1	0/1	0/1	0/1	0/1	.....
B. tectorum var. *glabratus* Spenner	.....	0/1	0/1	0/1	0/1	0/1	0/1	.....
B. vulgaris (Hook.) Shear	.....	0/1	0/1	0/1	0/1	0/1	0/1	.....
Dactylis glomerata L.	0/5	0/8	0/8	0/8	8/8	0/8	0/8	0/8
Danthonia parryi Scribn.	.....	.....	0/1	0/1	0/1	.....	.....	.....
D. semiannularis R. Br.	.....	.....	0/1	0/1	0/1	.....	.....	.....
Deschampsia caespitosa (L.) Beauv.	2/2	0/2	0/2	2/2	0/2	0/2	0/2	0/2
D. danthonioides (Trin.) Munro	.....	.....	0/1	1/1	0/1	0/1	1/1	.....
D. elongata (Hook.) Munro	.....	.....	0/1	0/1	0/1	.....	0/1	.....
Elymus canadensis L.	.....	0/5	0/4	0/5	0/5	0/4	0/5	0/2
E. condensatus Presl	0/1	0/4	0/4	0/4	0/4	0/4	0/4	0/1
E. dahuricus Turez.	0/1	0/1	0/1	0/1	0/1	0/1	0/1	0/1
E. glaucus Buckl.	.....	0/4	0/3	0/3	0/2	0/3	0/3	.....
E. junceus Fisch.	0/1	0/2	0/1	0/1	0/1	0/1	0/1	.....
E. sibiricus L.	.....	0/1	0/1	0/1	0/1	0/1	0/1	.....
E. triticoides Buckl.	.....	0/1	0/1	0/1	0/1	0/1	0/1	0/1
E. villosus Muhl.	.....	0/1	0/1	0/1	0/1	0/1	0/1	.....
E. virginicus L.	.....	0/4	0/4	0/4	0/4	0/4	0/4	.....
E. virginicus var. *glabriflorus* (Vasey) Bush	0/1	0/1	0/1	0/1	0/1	0/1	0/1	.....
E. virginicus var. *intermedius* (Vasey) Bush	.....	0/1	0/1	0/1	0/1	0/1	0/1	.....
Festuca arizonica Vasey	.....	.....	0/1	1/1	0/1	.....	0/1	.....
F. elatior L.	.....	0/1	0/1	0/1	0/1	0/1	0/1	.....
F. elatior var *arundinacea* (Schreb.) Wimm.	.....	0/1	0/1	0/1	0/1	0/1	0/1	.....
F. gigantea (L.) Vill.	.....	0/1	0/1	1/1	0/1	0/1	0/1	.....
F. idahoensis Elmer	.....	.....	0/1	0/1	0/1	0/1	1/1	0/1
F. obtusa Spreng.	.....	.....	0/1	0/1	0/1	0/1	1/1	.....
F. occidentalis Hook.	.....	.....	0/1	0/1	0/1	.....	1/1	.....
F. octoflora Walt.	1/1	.....	0/1	1/1	1/1	1/1	1/1	.....
F. ovina L.	.....	.....	0/1	1/1	0/1	0/1	1/1	.....
F. rubra L.	.....	0/1	0/2	0/2	0/2	0/1	0/2	.....
F. rubra var. *commutata* Gaud.	.....	0/1	0/1	0/1	0/1	0/1	0/1	.....
F. scabrella Torr.	.....	.....	0/1	0/1	0/1	0/1	0/1	.....
F. thurberi Vasey	.....	.....	0/1	0/1	0/1	.....	1/1	.....
F. viridula Vasey	.....	.....	0/1	0/1	0/1	.....	1/1	.....
Holcus lanatus L.	0/1	0/1	0/1	1/1	0/1	0/1	0/1	.....
Hordeum bulbosum L.	.....	0/1	0/1	0/1	0/1	0/1	0/1	.....
H. gussoneanum Parl.	.....	0/1	.....	0/1	0/1	0/1	.....	.....
H. jubatum L.	.....	0/1	.....	0/1	0/1	.....	.....	.....
H. jubatum var. *caespitosum* (Scribn.) Hitchc.	.....	0/1	0/1	0/1	0/1	0/1	.....	.....
H. murinum L.	.....	0/1	.....	.....	.....	.....	.....	.....
H. nodosum L.	.....	0/1	.....	0/1	0/1	0/1	0/1	.....
H. vulgare L.	0/1	0/2	0/2	0/2	0/2	0/2	0/2	0/2
Hystrix patula Moench	0/1	.....	0/1	0/1	0/1	0/1	0/1	0/1

TABLE 1.—(*Continued*)

Species tested[a]	Culture no. and source genus							
	Agrostis	*Avena*	*Avena*	*Polypogon*	*Dactylis*	*Bromus*	*Festuca*	*Koeleria*
	23	5	17	8	12	15	16	19
	Number of accessions infected[b]							
Koeleria cristata (L.) Pers.	4/5	0/5	0/7	6/7	0/7	0/5	0/7	6/6
Lolium multiflorum Lam.	0/1	0/1	0/1	0/1	0/1	0/1	0/1	0/1
L. perenne L.	0/1	0/1	0/1	0/1	0/1	0/1	0/1	0/1
Milium effusum L.	.....	0/1	0/1	1/1	0/1	.....	0/1	.....
Phalaris arundinacea L.	0/1	0/1	0/1	0/1	0/1	0/1	0/1	0/1
Phleum pratense L.	2/3	0/3	0/3	3/3	0/3	0/2	0/3	0/3
Poa ampla Merr.	.....	0/7	0/31	0/3	0/3	0/3	0/30	0/7
Poa arachnifera Torr.	.....	.....	0/1	0/1	0/1	0/1	0/1	.....
P. arctica R. Br.	.....	0/1	.....	.....	.....	.....	.....	.....
P. arida Vasey	.....	.....	0/1	.....	.....	.....	0/1	.....
P. bulbosa L.	.....	0/1	0/4	.....	.....	.....	0/4	0/1
P. canbyi (Scribn.) Piper	0/1	0/3	0/8	0/4	0/4	0/4	0/9	0/3
P. compressa L.	0/2	0/3	0/3	1/1	.....	.....	0/3	0/3
P. curta Rydb.	.....	0/1	0/1	1/1	.....	0/1	0/1	0/1
P. cusickii Vasey	.....	0/1	0/2	1/1	.....	0/1	0/2	0/1
P. epilis Scribn.	.....	0/1	0/2	0/1	0/1	0/1	0/2	0/1
P. gracillima Vasey	.....	0/1	0/3	0/2	0/1	0/2	0/3	0/2
P. interior Rydb.	.....	.....	0/1	0/1	0/1	0/1	0/1	.....
P. juncifolia Scribn.	.....	0/2	0/5	0/1	0/1	0/1	0/5	0/2
P. nemoralis L.	.....	0/3	0/8	0/5	0/3	0/5	0/4	0/1
P. nervosa (Hook.) Vasey	.....	.....	0/2	0/1	0/1	0/1	0/2	.....
P. nevadensis Vasey	0/1	0/3	0/6	.....	.....	.....	0/6	0/3
P. palustris L.	0/2	0/3	0/6	0/3	0/3	0/3	0/6	0/3
P. pratensis L.	0/4	0/14	0/15	1/7	.....	0/6	0/5	0/11
P. scabrella (Thurb.) Benth.	.....	0/1	0/3	0/3	0/3	0/3	0/3	0/1
P. secunda Presl	0/1	.....	0/6	0/3	0/4	0/3	0/6	0/3
P. sphondyloides Trin.	.....	0/3	0/5	0/1	0/1	0/1	0/4	0/3
P. sterilis Bieb.	.....	.....	0/1	0/1	0/1	0/1	0/1	0/1
Polypogon monspeliensis (L.) Desf.	0/1	.....	0/1	1/1	0/1	0/1	0/1	0/1
Puccinellia distans (L.) Parl.	0/1	.....	0/1	1/1	1/1	0/1	0/1	0/1
Secale cereale L.	0/2	0/1	0/1	0/1	0/1	0/1	0/1	0/1
Sitanion hystrix (Nutt.) J. G. Smith	0/1	0/1	0/1	0/1	0/1	0/1	0/1	0/1
S. jubatum J. G. Smith	0/1	0/1	0/1	0/1	0/1	0/1	0/1	0/1
Trisetum flavescens (L.) Beauv.	0/1	1/1	0/1	1/1	.....	.....	0/1	.....
T. spicatum (L.) Richt.	0/1	.....	0/1	0/1	0/1	.....	1/1	.....
Triticum aestivum L.	0/1	0/1	0/1	0/1	0/1	0/1	0/1	0/1

[a] Hitchcock (3) was followed wherever possible for the nomenclature of the grasses.
[b] Numerator of fraction refers to number of accessions infected; denominator refers to total number of accessions tested.

that Avena mildews are not necessarily restricted to species of *Avena*. The many negative results give a more complete understanding of the host range.

Culture 17. On Avena sativa, from Pullman, Washington

Culture 17, started from dry, infected leaves sent by Dr. George W. Fischer, infected *Avena brevis*, *A. fatua*, *A. nuda*, and *A. orientalis*. On varieties of *A. sativa* the following reactions were recorded: very susceptible

TABLE 2.—*Reactions of 39 accessions of grasses to 8 cultures of Erysiphe graminis*

Grass accessions[a]	Culture no. and source genus							
	Agrostis	*Polypogon*	*Avena*	*Avena*	*Dactylis*	*Bromus*	*Festuca*	*Koeleria*
	23	8	5	17	12	15	16	19
	Types of reaction[b]							
Agrostis exarata 21	4	2–3	0	0	0	0	0	0
Agrostis palustris 22	0	2–3	0	0	0	0	0	0
Alopecurus pratensis 234	0	3–4	0	0	0	0	.....	.....
Arrhenatherum elatius 23	0	3–4	0	1	0	0	0	0
Avena sativa 369	.....	0	4	4	0	0	0	0
Beckmannia erucaeformis 11	0	2	0	0	0	0	0	0
Beckmannia syzigachne 12	0–3–	3–4	0	0	0	0	0	0
Bromus carinatus 229	0	0	0	0	0	4	0	0
Dactylis glomerata 31	0	0	0	0	3–4	0	0	0
Deschampsia caespitosa 9	2+	3	0	0	0	0	0	0
Deschampsia caespitosa 10	3–	2	0	0	0	0	0	0
Deschampsia danthonioides 318	.....	3–	0	0	0	1	3–4	.....
Festuca idahoensis 250	.....	0	0	0	0	0	4	0
Festuca octoflora 323	4	2–	0	0	3–	0–1	4	.....
Festuca rubra var. *commutata* 85	.....	0	0	0	0	0	0	.....
Holcus lanatus 187	.....	2–3	0	0	0	0	0	.....
Koeleria cristata 32	2	1–2	0	0	0	0	0	3
Koeleria cristata 33	2	1+	0	0	0	0	0	2+
Koeleria cristata 34	0	1	0	0	0	0	0	4
Koeleria cristata 35	1	2–3	0	0	0	0	0	4
Milium effusum 223	.....	2–3	0	0	0	0	0	.....
Phalaris arundinacea 13	0	0	0	0	0	0	0	0
Phleum pratense 15	0	2–3	0	0	0	0	0	0
Phleum pratense 16	2–3	1–3	0	0	0	.....	0	0
Poa canbyi 43	0	.....	0	0	.....	.....	0	0
Poa compressa 49	0	.....	0	0	.....	.....	0	0
Poa compressa 50	0	2+	0	0	0	.....	0	0
Poa curta 51	.....	2–	0	0	0	0	0	0
Poa nevadensis 59	0	.....	0	0	.....	.....	0	0
Poa palustris 57	0	.....	0	0	.....	.....	0	0
Poa palustris 65	0	.....	0	0	.....	.....	0	0
Poa pratensis 68	0	0–1	0	0	0	0	0	0
Poa pratensis 69	0	0	0	0	.....	0	0	0
Poa pratensis 70	0	0	0	0	.....	.....	0	0
Polypogon monspeliensis 230	0	4	0	0	0	0	0	0
Puccinellia distans 251	0	2–	0	0	2+	0	0	0
Trisetum flavescens 228	0	2–3	3	0	0	.....	0	.....
Trisetum spicatum 329	0	0	0	0	0	.....	2+	.....

[a] Accession numbers assigned to grass collections by the writer.

[b] Classes of reaction expressed according to the system of Mains and Dietz (4):

0—Highly resistant. Little or no mycelium. Chlorotic or necrotic flecks on some hosts.

1—Very resistant. Slight to moderate mycelium. No sporulation. Chlorotic or necrotic spots may develop.

2—Moderately resistant. Moderate to abundant mycelium. Slight sporulation. Chlorotic or necrotic areas may develop.

3—Moderately susceptible. Moderate to abundant mycelium. Moderate sporulation.

4—Very susceptible. Abundant mycelium and sporulation.

..... — Indicates no test was made.

—Markton C.I. 2053, Richland C.I. 787, Boone C.I. 3305, Marion C.I. 3247, Bond C.I. 2733, Victoria C.I. 2401, Anthony C.I. 2143, Columbia C.I. 2820, D–67, C.I. 2870, Flughafer C.I. 3516, Fulghum C.I. 708, Gopher C.I. 2027, Green Mt. C.I. 1892, Hancock C.I. 3346, Iomine C.I. 2827, Makota C.I. 2885, Rainbow C.I. 2345, Ruakura C.I. 2025, Schwartzhafer C.I. 3520, White Tartar C.I. 551, Sterisel C.I. 2891, Victoria C.I. 1197 and White Tartar C.I. 3139; moderately susceptible—Iogold C.I. 2329, Erban C.I. 3477, Glabrota C.I. 2630, Landhafer C.I. 3522, Mutica Ukraina C.I. 3259, Richland C.I. 847, Fulton C.I. 3327, Bannock C.I. 2592, Red Rustproof C.I. 458, Marida C.I. 2571 and Joanette C.I. 2331.

A very resistant reaction on *Arrhenatherum elatius* was the only infection outside the genus *Avena*, and only 3 of 81 plants tested of this grass gave this reaction. The discrepancies between the results with Avena mildew obtained by previous workers in regard to the infection or non-infection of *A. elatius* could easily be attributed to the variability in *A. elatius* as well as to probable differences between the oat mildew cultures studied by each of the workers. *A. elatius* was also variable in its reaction to culture 8 from *Polypogon monspeliensis*. No variety of *Avena sativa* was resistant in the present study. *Trisetum flavescens* was uniformly, moderately susceptible to culture 5 and highly resistant to culture 17. On the basis of the reactions of this grass species to these two cultures pathogenic specialization is demonstrated in *Erysiphe graminis* from *Avena*.

Culture 12. On Dactylis glomerata, from Ann Arbor, Michigan

Culture 12 produced different types of infection on several accessions of *Dactylis glomerata* and moderately resistant reactions in *Festuca octoflora* and *Puccinellia distans*. The differences in reaction among accessions of *Dactylis glomerata* afford an opportunity to select for mildew resistance. This mildew culture probably represents a distinct specialized variety of *Erysiphe graminis*.

Culture 15. On Bromus carinatus, from Pullman, Washington

Culture 15 was started from infected plants sent by Dr. George W. Fischer and infected only a few species of *Bromus*. The very resistant reaction of *Festuca octoflora* furnishes the only evidence of infection outside the genus *Bromus*. Chlorotic spots were produced on *Deschampsia danthonioides* indicating that other susceptible grasses might eventually be found. The results in table 1 provide considerable negative evidence that has been lacking in all previously published records.

Culture 16. On Festuca idahoensis, from Pullman, Washington

Culture 16 was obtained from infected plants sent by Dr. George W. Fischer. It infected *Agrostis scabra, Deschampsia danthonioides,* various species of *Festuca*, and *Trisetum spicatum*. The species of *Festuca* varied in reaction from very susceptible to highly resistant. Certain species of *Festuca* were not infected by culture 16 but were susceptible to other cul-

tures which originated on other genera, *viz.*, culture 8 from *Polypogon* and cultures from *Poa* previously reported (2).

Culture 19. On Koeleria cristata, from Pullman, Washington

Culture 19 was collected in the Soil Conservation Service nurseries. It infected only collections of *Koeleria cristata*, and these differed in reaction. Three were very susceptible, two were moderately susceptible, and one was moderately resistant. *Festuca octoflora* and *Deschampsia danthonioides* were critical species to demonstrate infection outside the source genus for the cultures from *Bromus, Dactylis,* and *Festuca.* Unfortunately these two grasses were not available at the time culture 19 was studied.

Culture 8. On Polypogon monspeliensis, from Yakima, Washington

Culture 8 produced infection on many grass species of the genera in several tribes as follows: Tribe Festuceae—*Festuca, Poa,* and *Puccinellia;* Tribe Aveneae—*Arrhenatherum, Deschampsia, Holcus, Koeleria,* and *Trisetum;* Tribe Agrostideae—*Agrostis, Alopecurus, Milium, Phleum,* and *Polypogon;* and Tribe Chlorideae—*Beckmannia.* Culture 8 stemmed from a single pustule transfer, and a single colony isolation from this culture did not differ in host range. Therefore, culture 8 can be regarded as an individual race and not a mixture.

Culture 23. On Agrostis exarata, from Klickitat County, Washington

Culture 23 was started from infected, living plants sent by Dr. George W. Fischer. Infection was produced on *Agrostis alba, A. exarata, Beckmannia syzigachne, Deschampsia caespitosa, Festuca octoflora,* and *Koeleria cristata.* The infection of grasses in several tribes is somewhat similar to that produced by culture 8 from *Polypogon.* The two cultures are, of course, very different. Results with these two cultures and others suggest that there is probably a complex group of mildew races with overlapping host ranges affecting the grasses, especially *Agrostis, Phleum, Beckmannia,* and *Polypogon* in the tribe *Agrostideae.* Powdery mildew is commonly reported on these genera in the Pacific Northwest.

DISCUSSION

The various cultures differ in degree of specialization. Culture 8 from *Polypogon monspeliensis* infected 26 species of 17 genera in 4 tribes, and culture 23 from *Agrostis exarata* infected 7 species of 6 genera in 4 tribes of the Gramineae. *Erysiphe graminis* from *Avena, Bromus, Dactylis,* and *Festuca* have so far produced infection on a very few species outside the genus from which they were collected. Culture 19 from *Koeleria* infected only *Koeleria cristata.*

Certain cultures are comparable to previously described specialized varieties. Cultures 5 and 17 could be classed as *Erysiphe graminis avenae* and culture 15 as *E. graminis bromi.* If this system were continued mildew

cultures would be given varietal names based on the host genus from which they were collected. Since it was demonstrated previously (1, 2) and in the present study that most mildew cultures studied will infect species of two or more genera, two or several varietal names might be given to the same mildew race. Culture 12 from *Dactylis glomerata* could be named for either *Dactylis* or *Festuca*, and culture 16 from *Festuca idahoensis* might be named for *Festuca* or *Deschampsia*, depending upon the host genus from which the mildew races were obtained. Culture 8 from *Polypogon monspeliensis* and culture 23 from *Agrostis exarata* have wide host ranges. Grasses in several genera were distinctly susceptible to these two cultures, and thus several varietal names based on the source genus might be given to these two cultures, dependent again on the host genus on which these mildews are collected.

Many of these cultures, especially cultures 8 and 23, probably could be collected again on grass species of different host genera. Indiscriminate application of varietal names to races of *Erysiphe graminis* based only on the source genus can lead to repeated duplications, unavoidable synonyms, and unnecessary confusion. It would appear more desirable, at least for the present, to use laboratory or numerical designations for cultures of the fungus.

It is significant that all cultures of *Erysiphe graminis* from grasses outside the tribe Hordeae studied in the present investigation and previously reported from the genus *Poa* (2) infected only grasses outside this tribe. It was reported previously (1) that cultures studied from grasses in the tribe Hordeae infected only grasses in that tribe.

With the information now at hand there is little support for a concept of specialization of races of *E. graminis* to any given grass genus. In only a few cases was this noted, as follows: culture 20 from *Poa palustris*, previously reported (2), and culture 19 from *Koeleria cristata*. On the evidence of infection of species outside the source genus, obtained from the other cultures, it appears that even with cultures 19 and 20 other genera might have been infected if more collections and species had been tested.

Instead of narrow host specialization with restriction of infection of any mildew race to species of one genus as was believed and taught for over 40 years, since specialized varieties were distinguished by Marchal (5) in 1902, the situation regarding specialization of pathogenicity in *Erysiphe graminis* is quite the contrary for the most part. It has been demonstrated previously (1, 2) and in the present paper, that the majority of the races of *E. graminis* studied by the writer will infect species of two or more genera. With some cultures the host range is extensive, including many species and several genera.

Certain grasses are susceptible to several very different mildew races. The overlapping host ranges of different mildew races is such that powdery mildew occurring on some grass species might be any one race or a mixture of several mildew races The pathogenicity of mildew races occurring on

grasses in the tribe Hordeae has been previously described (1). In that study mildew cultures that infected barley were isolated from *Agropyron repens* and *Elymus dahuricus*. Another mildew culture that infected wheat was isolated from *E. dahuricus*. A mildew culture that infected barley and a few wild grasses and an Agropyron mildew that infected many wild grasses but not rye, wheat, or barley were found together as a mixture on *A. repens*. Another mixture on *E. dahuricus* contained a race that infected wheat and several wild grasses and a race that infected wild grasses, principally species of *Agropyron* and *Elymus*, but not wheat, barley, or rye. With this information we are better able to understand the origin of mildew outbreaks, particularly with reference to the sources of inoculum. Wild grasses can harbor wheat and barley mildews and supply the inoculum for infection of these cereals. Likewise mildew-infected wheat and barley companion crops with grasses, or fields of these cereals near grass stands, can be the sources of infection of grasses, especially species of *Agropyron* and *Elymus*. A probable illustration of the latter was observed by the writer during the early summer of 1940 in the Soil Conservation Service nurseries at Pullman, Washington. A heavily mildew-infected cover crop of wheat was adjacent to a grass observational row nursery containing many collections of species of *Agropyron* with very little infection. After about one week of wet weather a heavy outbreak of powdery mildew developed on many of the Agropyron species. The rapidity of the outbreak suggested a source of abundant inoculum, and the slight amount of infection already on the Agropyron species appeared to be an inadequate source. Circumstances pointed to mildew inoculum from the adjacent wheat cover crop.

Likewise, with accumulating information about the pathogenicity of other races of *Erysiphe graminis*, it will be easier to understand certain phases in the etiology of the disease on other grasses. A mildew outbreak occurred in western Oregon during 1941 on Chewings fescue, *Festuca rubra* var. *commutata*. Although a culture was not studied, there are certain facts that suggest mildew on *Poa pratensis* as a source of the outbreak. Mildew on *P. pratensis* is very common in the Pacific Northwest. One accession of Chewings fescue studied by the writer was very susceptible to mildew from *Poa pratensis* (2), but was resistant to mildew from *Festuca idahoensis*.

Another example was an outbreak of mildew on *Phalaris arundinacea* near the college golf course at Pullman, Washington, reported to the writer by Dr. George W. Fischer. *P. arundinacea* is seldom reported infected by mildew. When informed that the writer had produced infection on *P. arundinacea* with mildew from *Poa pratensis*, Dr. Fischer replied that this could very possibly have been the source of the outbreak, since *P. pratensis* was the only other grass infected with mildew within a considerable distance of the area.

Although the relationships in these examples are based largely on field observations, they are supported by experimental evidence. The writer believes that these examples offer plausible explanations of mildew outbreaks

on certain grasses, and with the accumulating information about the host ranges of additional mildew races, such reasoning should aid in understanding certain phases in the epiphytology of the disease.

While nothing conclusive has been reported concerning the sexual nature of *Erysiphe graminis* and although hybridization between races is a theoretical suggestion, the fact that so much variation is found in this species is ample evidence of the genetic segregations which have already taken place. There are opportunities for hybridization between widely different races, since certain grass species are susceptible to a number of races. In a study of the mildew races attacking grasses in the tribe Hordeae (1) it was demonstrated that mildews which infect barley, wheat, *Agropyron*, and *Elymus* can all occur together on the same grass, especially on certain species of *Agropyron* and *Elymus*. The situation with other mildew races is comparable. For example, *Festuca octoflora* is susceptible to mildew races from *Agrostis, Dactylis, Festuca*, and *Poa* and to a lesser extent also to races from *Polypogon* and *Bromus*. *Koeleria cristata* is susceptible to mildew races from *Poa, Koeleria, Polypogon*, and to a lesser extent also from *Agrostis*. Many other examples could be given in which grasses are susceptible to two or more mildew races. All of these grasses are potential sites for hybridization between races that may be widely different pathogenically. Considering these possibilities it is not surprising to find great variation for pathogenicity among races in *Erysiphe graminis*.

Results on specalization suggest that there have been genetic segregations in *Erysiphe graminis* that have established themselves on certain grass species. In studies of pathogenic specialization probably only a few of these segregates have been studied. That some appear to be narrowly specialized and others less so is important, but viewing *E. graminis* as a broad species comprising many genetic combinations and constantly producing new segregates, we may anticipate descriptions of additional new races that cannot be readily classified on the basis of a varietal system of classification.

SUMMARY

Selected groups of 360 accessions of 123 species and 8 varieties of grasses in 28 genera were inoculated with 8 cultures of *Erysiphe graminis* from grasses outside the tribe Hordeae as follows: 2 cultures from *Avena* and one culture each from *Agrostis, Bromus, Dactylis, Festuca, Koeleria*, and *Polypogon*.

Seven of the cultures infected grass species outside the genus from which they were collected. Powdery mildew from *Koeleria cristata* infected only this species.

Two cultures from *Avena sativa* were different pathogenically, and pathogenic specialization is therefore demonstrated in *Erysiphe graminis* from *Avena*. No variety of *A. sativa* was resistant in the present study.

Many grass species are susceptible to two or more widely different mildew races and thus perhaps may present the opportunity for hybridization between races.

Certain races may perhaps bear varietal names to advantage if they continue to have distinctly narrow specialization. Several mildew cultures have wide host ranges, and a varietal designation for such races appears to be impracticable.

Variation in mildew reaction between collections of most grass species and between individual plants in many collections affords ample opportunity to select for mildew resistance.

Erysiphe graminis occurring on a given grass species can no longer be automatically assumed to be a specialized variety restricted in infection to species of the source genus. On the contrary, inoculation results demonstrate that it may be any one of a number of mildew races or a mixture of races.

The evidence of a general lack of specialization of mildew races to any given genus permits recognition of the possibilities of hybridization between races, the possible sources of inoculum in the initiation of mildew infections, and explanations of certain phases of the etiology and of the epiphytology of the disease.

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THE SEASONAL DEVELOPMENT AND THE DEFOLIATING EFFECT OF CRONARTIUM RIBICOLA ON NATURALLY INFECTED RIBES ROEZLI AND R. NEVADENSE

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INTRODUCTION

Ribes roezli and *R. nevadense* are the two principal ribes species associated with sugar pine in the California sugar pine region. Since this region differs not only in host species but also in weather characteristics from other parts of North America where experience with white pine blister rust has been gained, the development of the rust on these host plants and their responses in the existing environment are of particular interest and concern in the rust control problem here.

The relative susceptibility of these two species was studied earlier on bushes transplanted into British Columbia (6). *Ribes nevadense* was rather susceptible in comparison with other western ribes species (4) and produced many telia, while *R. roezli* was extremely susceptible but shed its infected leaves early. Therefore, it produced few telia. With the appearance of rust in California, it was possible in 1938, 1941, and 1943 near Montgomery Creek and Hatchet Creek to observe the development of the rust on these species in their native habitat, and to correlate this with the danger to neighboring sugar pines. Some critical details are herein reported.

METHODS AND BASES

Representative infected plants of *Ribes roezli* and *R. nevadense*, varying in degree of initial infection, and growing under varying site moisture conditions and exposure to direct sunlight, were selected for observation. On extremely large plants detailed data were taken only on one or two large representative branches rather than on the entire plants.

Detailed data on host and rust development and reaction were taken separately for each plant or each branch selected. Biweekly examinations were made from July, when nearly all leaves were formed and the rust was becoming well established, to late October, when nearly all leaves had dropped.

In 1938 a total of 100 plants of *Ribes roezli* and 8 of *R. nevadense* scattered over both Montgomery Creek and Hatchet Creek drainages were

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observed. The ribes that became infected with *Cronartium ribicola* that spring were infected by aeciospores blown from distant northern pine infections. During the year aeciospores of the pinyon rust, *Cronartium occidentale*, apparently were blown into this locality from the south. Only 43 of the 100 selected plants of *R. roezli* were infected with *C. ribicola*, as determined by differential staining of telial columns (1, 2), the most satisfactory method known for differentiating between the two rusts on ribes. By 1941 and in 1943 there were aeciospore-producing sugar pine infections on the study areas. In 1941 rust samples from each of the 65 plants of *R. roezli* and 10 of *R. nevadense* selected on the Montgomery Creek area were tested microchemically and determined as *C. ribicola*. The 62 plants of *R. roezli* and the 18 of *R. nevadense* selected in 1943 on the Hatchet Creek area were scattered about two infected sugar pines bearing abundant aecial cankers, so it was not considered necessary to test rust samples from each plant. All samples tested from 20 plants were *C. ribicola*. No *C. occidentale* was found in these localities in 1941 or 1943.

The amount of live-stem (living branchwood) expressed in linear feet is a measure commonly used by blister rust workers for ribes. The data herein are presented on this same unit basis.

RESULTS

The weather in 1943 was similar to that in 1938 and there was great similarity in the rust development on ribes and its effect on ribes defoliation in these two years. Because of the similarity, many of the data of 1938 are omitted in tables and figures. However, the general results and conclusions herein reported are based upon the observations in 1938 as well as those in 1941 and 1943.

Weather

Spring weather favored infection of ribes from aeciospores in each of the three test years. This was not the case in some of the intervening years, particularly in 1942. Although the initial ribes infection in 1938 was not heavy, late spring rains favored intensification of the rust. There were no summer rains in 1938, and there was no rain from June 21 to October 11 in 1943, but the summer of 1941 was abnormally cool with comparatively frequent rains (Table 1).

TABLE 1.—*The distribution of rainfall in Montgomery Creek and Hatchet Creek areas in California from July through October in 1938, 1941, and 1943*

Month	Dates on which rainfall occurred		
	1938	*1941*	*1943*
July	.....	15–16–17	.....
August	.....	15–16–29–30	.....
September	27–28	1–2–12–18–19	.....
October	1–15–16–23–28–29–30	10–12–19–20–26–27–28	11–17–18–19–20–21–22–23–24

Ribes Defoliation

The very wet May of 1941 provided good conditions for initial ribes infection from pines, and the abnormally frequent summer rains intensified the rust infection on the ribes leaves. On *Ribes roezli* the intensity of the rust infection caused considerable premature leaf-fall. This early dropping of leaves and the abundance of moisture stimulated the formation of new leaves throughout the season on this species. The average extent of new leaf formation and the average leaf-fall for infected and uninfected leaves of this species throughout the 1941 season are in table 2. The plants have been divided into light forms: the open-form plants are those that received very little or no shade; the part-shade-form plants received shade and direct sunlight in about equal proportions; and the shade-form plants received little or no direct sunlight. The open-form plants bore the most leaves per hundred feet of live stem and the shade-form plants the least. The fewer leaves on the part-shade and shade-form plants were largely compensated for by their larger size, making leaf area per hundred feet of live stem nearly equal on all forms. Premature leaf-fall was greatest on the open-form plants and least on the shade-form plants. Precocious leaf-fall induced by the rust infection is generally more severe on gooseberries than on currants (5, p. 42). On *Ribes nevadense* premature leaf-fall was not great and the formation of new leaves during the summer was negligible (Table 2). Open-form plants of *R. nevadense* were practially nonexistent on the study areas, because cattle readily browse on this smooth-stemmed species wherever the plants are not protected or screened by other vegetation. Observations on the open-form plants of this species have not been included.

Table 3 shows the average leaf-fall in 1943 when there were no summer rains. The last spring rain, on June 21, caused the only pronounced wave of rust intensification on *Ribes roezli*. Rust development is considerably slower on *R. nevadense* than on *R. roezli* and by June 21 the uredia on *R. nevadense* were not developed sufficiently to cause heavy intensification of the infection. The part-shade and shade-form plants of *R. roezli* did not produce the amount of intensification from the June 21 rain that the open-form plants did (Table 3). This was due to the fact that the development of the uredia on these shaded plants was not so advanced as that on the open-form plants by June 21. Table 3 also shows how this heavier intensification of the rust on the open-form plants caused much greater premature leaf-fall than occurred on the shaded plants. The premature leaf-fall of *R. roezli*, in general, was not so great in 1943 as in 1941 because there were no summer rains to intensify the infection. However, the lack of summer rains probably hastened the normal dropping of uninfected leaves, and on most plants the infected leaves were shed before the uninfected leaves. When soil moisture for individual plants is considered, the number of new leaves formed on *R. roezli* during the summer of 1943 fairly well depicts the severity of the premature leaf-fall. The formation of the new

leaves on *R. nevadense* in 1943 was largely stimulated by the premature leaf-fall caused by insects and anthracnose rather than by blister rust infection.

TABLE 2.—*Average progressive leaf-fall per hundred feet of live stem for both infected and uninfected leaves for each light form of Ribes roezli and R. nevadense at the Montgomery Creek Area in 1941*

Species, light form, and date observed		Number of leaves per 100 feet of live stem			Number of infected leaves per 100 feet of live stem			
		Total dropped	Formed since previous exam.	Total attached	Total dropped	Remaining from previous exam.	Infected since previous exam.	Total attached
Ribes roezli								
Open	July 26–29	352	.....	2687	201	.....	.....	1246
	Aug. 12–14	1583	113	1570	1352	365	1030	1125
	Aug. 25–27	2280	63	918	2040	450	233	658
	Sept. 9–10	2754	61	505	2462	237	99	334
	Sept. 23–24	3013	14	258	2656	139	21	160
	Oct. 7–8	3196	9	84	2786	30	9	39
	Oct. 23	3243	5	42	2814	10	0	10
Part shade	July 26–29	243	.....	2303	176	.....	.....	1223
	Aug. 12–14	948	48	1646	869	603	745	1275
	Aug. 25–27	1677	20	937	1563	653	116	697
	Sept. 9–10	2072	23	566	1931	330	49	378
	Sept. 23–24	2283	16	370	2097	212	18	230
	Oct. 7–8	2541	1	113	2279	51	10	58
	Oct. 23	2636	0	18	2334	4	1	4
Shade	July 26–29	217	.....	2018	150	.....	.....	974
	Aug. 12–14	805	48	1479	735	416	762	1151
	Aug. 25–27	1301	29	1004	1231	649	75	724
	Sept. 9–10	1616	28	717	1535	420	67	488
	Sept. 23–24	1842	10	502	1731	291	20	312
	Oct. 7–8	2127	1	218	1965	84	51	129
	Oct. 23	2300	0	45	2078	16	0	16
R. nevadense								
Part shade	July 26–29	16	.....	1704	5	.....	.....	378
	Aug. 12–14	147	0	1573	63	320	1070	1390
	Aug. 25–27	329	0	1390	245	1208	114	1323
	Sept. 9–10	640	0	1079	556	1012	5	1017
	Sept. 23–24	871	0	848	787	786	30	815
	Oct. 7–8	1325	0	394	1241	362	15	377
	Oct. 23	1689	2	32	1602	16	0	16
Shade	July 26–29	51	.....	1979	2	.....	.....	846
	Aug. 12–14	141	0	1889	84	764	306	1071
	Aug. 25–27	243	1	1788	186	968	163	1131
	Sept. 9–10	436	0	1595	379	938	99	1037
	Sept. 23–24	882	0	1150	825	591	183	775
	Oct. 7–8	1428	0	603	1273	328	56	383
	Oct. 23	1919	0	112	1593	63	0	63

The first frosts in the autumn appeared to affect the fall of infected leaves of *Ribes roezli* more than uninfected leaves. Later frosts were so severe that both uninfected and infected leaves dropped. There appeared to be little difference in effect of frost upon the leaf shedding of *R. nevadense*

whether infected or not. Light early frosts caused the dropping of few leaves of this species and later heavy frosts caused many leaves to fall.

TABLE 3.—*Average progressive leaf-fall per hundred feet of live stem for both infected and uninfected leaves for each light form of Ribes roezli and R. nevadense at the Hatchet Creek Area in 1943*

Species, light form, and date observed		Number of leaves per 100 feet of live stem			Number of infected leaves per 100 feet of live stem			
		Total dropped	Formed since previous exam.	Total attached	Total dropped	Remaining from previous exam.	Infected since previous exam.	Total attached
Ribes roezli								
Open	July 16–19	10	.....	3395	10	.....	.....	2130
	July 28–31	617	28	2785	614	1506	280	1787
	Aug. 13–16	1724	12	1690	1705	696	541	1236
	Aug. 27–28	2273	11	1141	2254	679	113	792
	Sept. 10–11	2819	23	618	2750	296	0	296
	Sept. 24–25	3019	13	431	2907	139	0	139
	Oct. 9	3109	11	352	2973	73	0	73
	Oct. 24	3252	2	210	3016	30	0	30
Part shade	July 16–19	47	.....	2859	47	.....	.....	1340
	July 28–30	371	11	2545	371	1016	95	1111
	Aug. 13–16	820	5	2102	718	765	208	973
	Aug. 27–28	1258	2	1666	1117	575	45	620
	Sept. 10–11	1636	0	1288	1422	315	0	315
	Sept. 24–25	2042	1	883	1564	173	0	173
	Oct. 9	2353	0	572	1654	83	0	83
	Oct. 24	2775	0	150	1728	9	0	9
Shade	July 17–19	32	.....	2445	30	.....	.....	635
	July 29–31	74	22	2425	72	592	16	608
	Aug. 13–16	218	10	2291	204	476	300	776
	Aug. 27–28	404	1	2106	390	591	21	612
	Sept. 10–11	773	1	1737	731	271	0	271
	Sept. 24–25	1265	1	1261	878	126	0	126
	Oct. 9	1662	1	866	963	40	0	40
	Oct. 24	2217	0	311	991	12	0	12
R. nevadense								
Part shade	July 16–19	2	.....	1495	1	.....	.....	358
	July 28–31	145	8	1361	97	262	59	321
	Aug. 13–16	248	1	1261	152	266	89	355
	Aug. 27–28	378	1	1138	186	323	38	361
	Sept. 10–11	473	2	1045	234	313	0	313
	Sept. 24–25	629	2	892	294	253	0	253
	Oct. 9	804	0	717	352	196	0	196
	Oct. 24	1089	0	432	427	121	0	121
Shade	July 16–19	2	.....	1149	2	.....	.....	340
	July 29–31	43	5	1113	10	332	4	336
	Aug. 13–16	48	2	1110	15	331	71	402
	Aug. 27–28	66	0	1091	33	383	8	392
	Sept. 10–11	94	0	1064	61	364	0	364
	Sept. 24–25	217	0	942	160	265	0	265
	Oct. 9	397	0	762	259	166	0	166
	Oct. 24	509	0	649	294	131	0	131

Beside frosts, severity of infection, and degree of exposure of the plants to direct sunlight, two other factors influenced premature leaf-fall of infected *Ribes roezli*. One of these was the soil moisture of the site. The more moist

the site the more retentive were the infected leaves when the severity of infection was the same. However, on wet sites the infection usually was more severe, because the leaves were more succulent and therefore more susceptible to attack by the rust, and dews that promoted rust intensification often occurred on such sites. Another influential factor, aside from site conditions, was the character of the leaves. Young, thrifty leaves on current season's growth were much more retentive than older leaves, or leaves on wood of previous growth. The last leaves to drop from a plant were always from branch growth of the current season. The infected leaves of *R. roezli* that were the last to drop in the autumn were the tip leaves on current growth of shade-form plants growing on moist sites.

Rust Development

Although the initial infection on ribes in 1938 was somewhat lighter than in 1941 and 1943, because of the greater distance from the aecial source, there were several well-distributed rains in June, 1938, that caused considerable intensification of the rust. By July and August the amount of rust was about equal to the amount present at this same time in 1943. In 1941, however, rains permitting uredial intensification were not only abundant during the spring months but also continued to occur frequently throughout the summer. However, the greater premature leaf-fall of *Ribes roezli* in 1941, caused by the heavier rust infection, prevented the rust on that species from building up to a much greater amount than in 1938 and 1943. The premature leaf-fall on *R. nevadense* in 1941 was less excessive, and the rust on that species built up much more than in the other two years. Figure 1 shows the amount of rust, per foot of live stem, present on the ribes plants throughout the 1941 season. Figure 2 shows the development of rust in 1943. These figures also show the amount of infected leaf surface bearing telia, the portion of the telia that was viable, and the time that weather probably favorable for pine infection occurred. A considerable number of telia germinated, as a result of the summer rains in 1941, before the leaves were dropped, whereas in the absence of summer rains in 1943 telia usually remained viable until the infected leaves were dropped. Although most telia on leaves of *R. nevadense* remained viable until rain occurred, some died before; the telia that did not remain viable until the rain of October 11 in 1943 had not germinated but had died, usually as a result of the death of large infected portions of the leaf. Although infected leaf portions died before and after uredia were developed on both ribes species, infected leaf portions bearing telia on *R. roezli* never died before the leaves were dropped. On some plants of both species practically all infected leaf tissue died before producing telia. Very short, dark, abortive columns of telia, with little or no evidence of viability, were found in 1938 on the small, thick, coarse leaves of a few open-form plants of *R. roezli* growing on dry sites. Such abortive telial columns were rarely seen in 1941 and 1943. The percentage of the infected leaf surface that produced telia was higher in *R. roezli* than in *R. nevadense* and would have been higher still had consider-

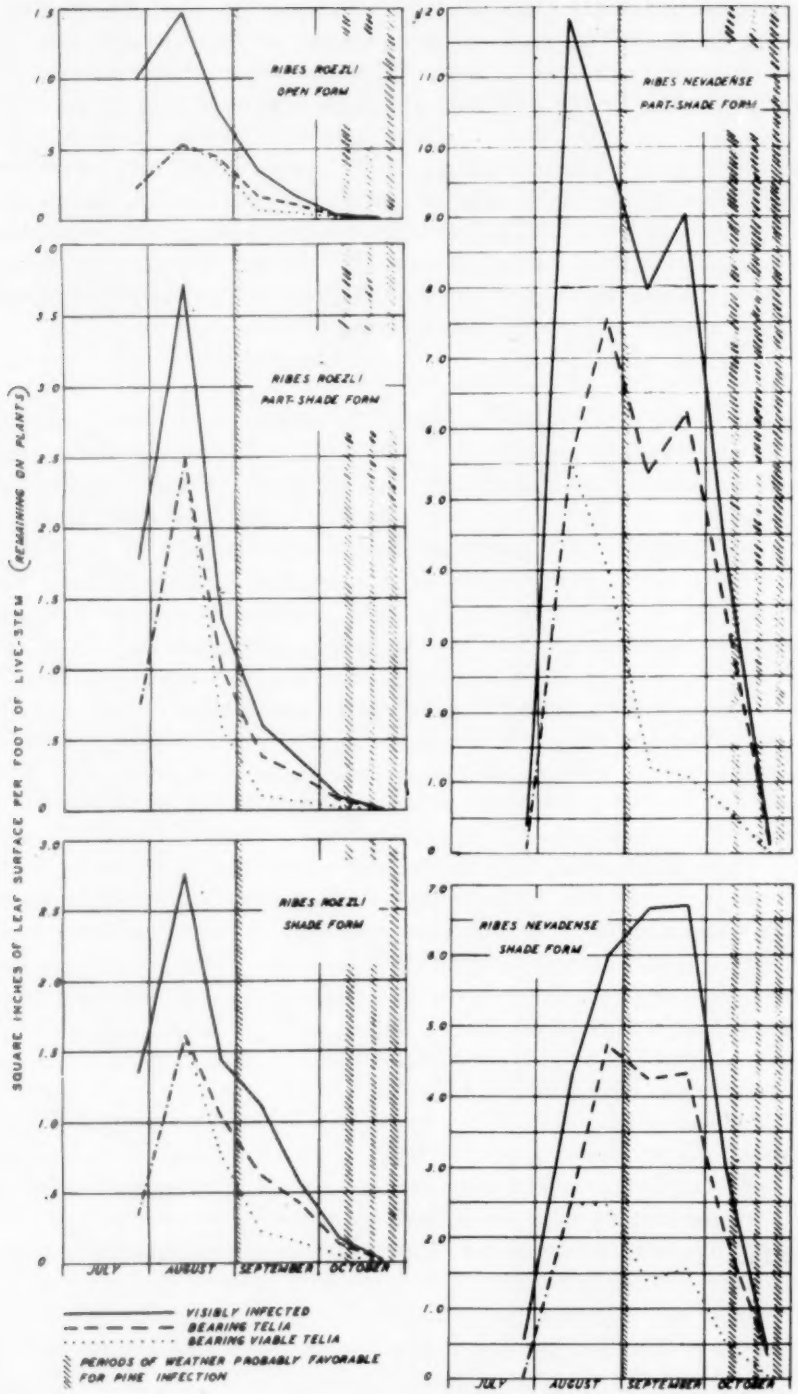

FIG. 1. Average blister rust development on plants of the various light forms of *Ribes roezli* and *R. nevadense* at the Montgomery Creek Area in 1941. (All telia were viable in some cases, as indicated by the complete overlapping of the dot and dash lines.)

able uredial infection not been lost by premature leaf-fall. In addition to producing a higher percentage of telia, the infected leaves of *R. roezli* had nearly twice the number of telial columns per unit of telial-bearing leaf area that the infected leaves of *R. nevadense* had. Telial counts, through

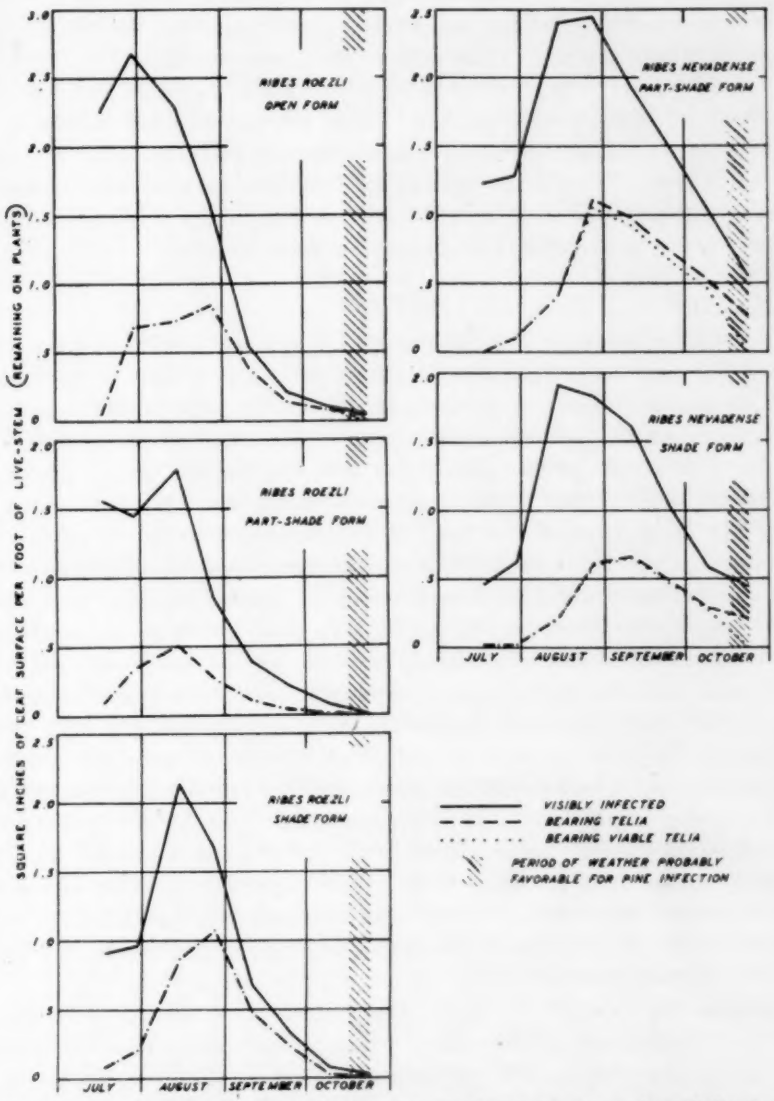

FIG. 2. Average blister rust development on plants of the various light forms of *Ribes roezli* and *R. nevadense* at the Hatchet Creek Area in 1943. (All telia were viable in many cases, as indicated by the complete overlapping of the dot and dash lines.)

a microscope, made on 36 typical specimens for each species, showed that an average square inch of telia-bearing leaf surface of *R. nevadense* contained approximately 4,600 telial columns, while that of *R. roezli* contained 8,700 telial columns.

General observations on other naturally infected *Ribes roezli* and *R. nevadense* over a number of years and at various localities and data and observations on plants used in other blister rust studies, under controlled infection conditions, have been in accord with the findings herein reported. There is a great variation in susceptibility between plants of *R. roezli*, greater variation than for any other ribes species tested in the West. Many plants were not infected while adjoining plants were severely infected. Some plants exposed to an abundance of aeciospores or urediospores under controlled infection conditions have never become infected in any visible degree, whereas other plants have become severely infected under less favorable conditions. There is an indication, from the various tests made, that in the northern range of *R. roezli* a greater percentage of plants have this high resistance to infection than in its southern range.

DISCUSSION

For ribes to cause pine infection it is necessary that they have viable telia at the time of a favorable moisture period of sufficient duration to bring about germination of teliospores, the development of the promycelia, the formation and dispersal of the sporidia, the germination of the latter, and the penetration of the germ-tubes into the needles of the host. The time required for these processes varies with the air temperature and the age of the teliospores at the time of the favorable moisture period. At favorable temperatures 24 to 36 hours are required for appreciable pine infection, during which high humidities must prevail in order to maintain the necessary free moisture (5, p. 33). In most parts of the sugar pine region this would occur only during rainfall, but in small localized areas, following a short but heavy rain, free moisture may be retained sufficiently long on ribes plants and pine foliage that are well shaded by a high canopy and further sheltered from wind and sun by dense surrounding brush and other vegetation. Such areas are on sheltered north slopes or on wet sites where a heavy night dew often follows a heavy rain. Pine probably will not become infected at temperatures below 32° F., and below 50° F. a progressively longer time is required (3). For this reason periods of snowfall usually are not favorable for pine infection, and late autumn rains often occur when the air temperature is so low that the period required for pine infection is much greater.

Moisture for less than 24 hours often induces germination of teliospores without the subsequent infection of pines. Short rains usually intensify the rust on the ribes plants, through germination of urediospores on the leaves, and incite the development of new telia.

Both *Ribes roezli* and *R. nevadense* had sufficient viable telia to serve as a source for considerable pine infection at the time of favorable rains in 1938 and 1941; however, in 1943 the light shower on October 11 may have induced germination of some of the few remaining teliospores on *R. roezli*, without subsequent pine infection, before the favorable rains starting on October 17. Even if this earlier rain did not dissipate teliospores, a smaller amount

of viable telia remained on leaves of *R. roezli* on October 17 than occurred on this species at the time of favorable rains in 1938 and 1941. Telia remaining on *R. nevadense* on October 17, however, were still sufficient for considerable pine infection even if partly dissipated by the October 11 rain. Observations in the three years indicate that when there are no summer rains to maintain a supply of uredia it is possible that little or no pine infection will occur if the first autumn rain dissipates the telia, but does not provide ample time for subsequent pine infection. With relatively frequent summer rains, however, it is probable that sufficient uredia will be present to cause intensification of the rust, with the subsequent production of new telia on the ribes, so that there will still remain a chance for pine infection at the time of later rains. If the first rain occurs after mid-October it appears likely that only plants of *R. nevadense* and the shade form of *R. roezli* will have enough leaves to provide the requisite inoculum. The success or failure of the rust to infect pines during any year will depend largely on whether or not a rain of sufficient duration occurs before ribes defoliation, whether the defoliation be caused by heavy rust infection, drought and hot weather, or heavy frosts. Under infection and weather conditions similar to those on the study areas in any of the three test years *R. roezli* will bear adequate inoculum for pine infection at any time from late-July to late-September, and with the shade-form plants growing on moist sites this period may be extended to mid-October. Under similar conditions *R. nevadense* may provide inoculum for pine infection from early-August to late-October.

It appears then, from all observations, that with heavy rust infection, either from abundant aecial sources, or as a result of weather conditions favorable for rust intensification, per foot of live-stem, *Ribes nevadense* will be the more important host of the two ribes species concerned. Even with less severe infection *R. nevadense* will be of more consequence when the autumn rains are late. Per foot of live-stem, *R. roezli* will be of greater importance only under conditions of less severe infection when summer or early autumn rains occur and are of sufficient duration for pine infection. Blister rust control workers have found that on the average approximately 2,900 feet of *R. roezli* live-stem and 420 feet of *R. nevadense* live-stem occur per acre within the California sugar pine region before eradication. Therefore on average unworked areas it is most probable that the larger population of *R. roezli* plants, and this species' greater production of telial columns per unit of leaf surface bearing telia, will make it the more dangerous one, unless the first rain suitable for pine infection occurs after mid-October.

SUMMARY

As an aid to planning control of white pine blister rust in the California sugar pine region, observations were made on the development and defoliating effect of this disease on naturally infected plants of *Ribes roezli* and *R. nevadense* in their native habitat in the northern Sierra Nevada in 1938, 1941, and 1943.

Infected plants varying in degree of initial infection and growing on

different sites were examined biweekly and detailed data were taken on host and rust development and reaction from July to October, inclusive, each year.

In general, the susceptibility of the two ribes species to infection by the rust and the telium-producing capacity of *R. nevadense* were the same as reported from earlier studies in British Columbia and the Pacific Northwest; but *R. roezli* produced considerably more telia, because fewer infected leaves were dropped before telia were developed. Although *R. roezli* remained the more susceptible of the two species and its infected leaf area produced a higher percentage of telium-bearing surface and nearly twice the amount of telial columns per unit of telium-bearing surface, the premature dropping of its infected leaves still prevented it from being as dangerous a pine-infecting species as *R. nevadense* per unit of population. In unworked areas of the California sugar pine region *R. roezli* is the more potentially dangerous species because its greater population more than counterbalances its limited capacity to retain telium-bearing leaves.

Severity of infection, site conditions, character of infected leaves, and occurrence of autumnal frosts appeared to be the more significant factors influencing premature fall of infected leaves of *Ribes roezli*. Only severe infection and heavy autumnal frosts caused appreciable premature fall of infected leaves of *R. nevadense*.

Infected plants of *Ribes roezli* growing under shade and producing abundant new woody growth, especially plants on moist sites, are potentially the most dangerous of this species with respect to spread of blister rust. The tip leaves of the current season's growth on such plants were the last to drop in the autumn, and consequently urediospores and viable telia remained latest on this type of leaf.

Many infected leaves of *Ribes nevadense* were present on the plants at the time of the first favorable autumnal rains.

The time of year that rain occurs in sufficient duration to provide for pine infection will determine the success or failure of the rust, from either ribes species, to infect pines in a given year.

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AECIAL HOSTS OF PUCCINIA GRAMINIS IN CHINA

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The susceptibility and resistance of the Berberidaceae to *Puccinia graminis* Pers. have been extensively studied in the Minnesota Agricultural Experiment Station in the United States. In the summarized account by Levine and Cotter,[2] 28 species of *Berberis* indigenous to China were listed, among which 27 are susceptible and one apparently immune. In a more recent list of Stakman,[3] 8 additional Chinese species were included. In 1905, Baccarini[4] on the basis of specimens collected from Shensi, China, considered *Epimedium*, in addition to 2 species of *Berberis*, as the host of *P. graminis*. He apparently mistook the aecial stage of *Puccinia epimedii* (Henn. et Shir.) Miyabe et Ito for *P. graminis*. As China, especially in the Himalaya ranges, is known to be the native country of a large number of species of *Berberis* and *Mahonia*, the knowledge so far gathered regarding the alternate hosts of stem rust appears to be far from complete. Consequently, many specimens representing about 50 species of *Berberis* and 15 of *Mahonia* have been examined for rust infection in the following herbaria of China: National Central University; University of Nanking; National Szechuan University; Institute of Agricultural Research, National Tsing Hua University; Biological Laboratory of the Science Society of China; and Szechuan Provincial Agricultural Improvement Institute. Field observations also have been made in the western part of Szechuan province.

As a result of herbarium examination and field observations, 12 species of *Berberis* and 1 of *Mahonia* have been found harboring the aecial stage of *Puccinia graminis* (Table 1). Three of them, *B. silva-taroucana* Schn., *B. virgetorum* Schn., and *M. fortunei* (Lindl.) Fedde, are hitherto unrecorded as carriers and breeders of stem rust. It is even more interesting to note that *B. gagnepainii* Schn., *B. julianae* Schn., and *B. sargentiana* Schn. are classed in the list of Stakman as immune or highly resistant in the spring wheat region in the United States, but conspicuous infections have been noticed on the specimens in China. Another species, *B. dielsiana* Fedde, according to the results of artificial inoculations made by Levine and Cotter in Minnesota, is attacked only lightly by *P. graminis secalis* Erikss. et Henn. and not at all by *P. graminis tritici* Erikss. et Henn. This species, however, is the one most common in the mountain region (sungshan) of northern

[1] Phytopathology extends the courtesy of its journal pages to scientists in other countries who are persevering in research under difficult wartime conditions and are temporarily deprived of the opportunity for membership in the American Phytopathological Society.

[2] Levine, M. N., and R. U. Cotter. Susceptibility and resistance of *Berberis* and related genera to *Puccinia graminis*. U. S. Dept. Agr. Tech. Bull. 300. 1932.

[3] Lehmann, E., H. Kummer, and H. Dannenmann. Der Schwarzrost. 584 pp. J. F. Lehmanns Verlag, München/Berlin. 1937.

[4] Baccarini, P. Funghi dello Schensi septentrionale raccolti dal Padre Giuseppe Giraldi. App. al. Nuovo Giorn. Bot. Ital. 22 (nuova serie): 689–698. 1905.

TABLE 1.—*Aecial hosts of Puccinia graminis in China based upon field and herbarium observations*

Species	Localities where rusted specimens were collected	Known distribution in China
Berberis acuminata Fr.	Kunming, Yunnan	West Szechuan, Yunnan
B. amurensis Rupr.	Wulingshan, Hopei	Hopei, Shansi, Mongolia Manchuria
B. dielsiana Fedde	Sunghsien, Honan	Honan, Shensi, Szechuan
B. gagnepainii Schn.	Mt. Omei, Szechuan	West Szechuan, Sikang
B. henryana Schn.	Chengkow, Szechuan	East Szechuan, west Hupeh, Anhwei
B. julianae Schn.	Wantsaoshan, Hupeh	Hupeh, Yunnan, Shensi
B. levis Fr.	Mt. Omei, Panlanshan, and Kwanhsien, Szechuan	West Szechuan, Yunnan, Sikang
B. pruinosa Fr.	Chengkiang, Tungchwan, and Süanwei, Yunnan	Yunnan
B. sargentiana Schn.	Suon Nai Ook, Hupeh	West Hupeh
B. silva-taroucana Schn.	Mt. Omei, Szechuan	West Szechuan, Sikang
B. virgetorum Schn.	Kuling, Kiangsi	Kiangsi, Kwangtung
B. wilsonae Hemsl.	Lifan, Szechuan	West Szechuan, Sikang, Yunnan
Mahonia fortunei (Lindl.) Fedde	Mt. Omei, Szechuan	Szechuan, Sikang, Hupeh

Honan province and is usually severely rusted by *P. graminis*. This probably indicates that certain physiologic races are virulent and that those species which have been considered immune or resistant in America probably could not be introduced and distributed there with entire safety. *B. sargentiana*, which has been recommended[5] as one of the most desirable for

FIG. 1. Aecial infection of *Puccinia graminis tritici* on *Berberis levis*.

[5] Sargent, C. S. (editor). Plantae Wilsonianae. Publication of Arnold Arboretum No. 4. Vol. 1. 1913. Vol. 3. 1917.

introduction as a garden plant to the United States because it was perfectly hardy in the Arnold Arboretum, probably should be regarded with caution.

The Province of Szechuan is bounded by mountain ranges of moderate height (1,500 to 3,000 meters) mostly; but along the western and northwestern edges some extremely high peaks and ranges, mostly unexplored and unsurveyed, appear to be from 5,000 to 7,000 meters high. In those western ranges, the richness of *Berberis* and *Mahonia* is well known. E. H. Wilson alone collected 31 species and varieties of those two genera there.[5] The hollow land in the center of the province has been named by geographers the Red Basin of Szechuan, where wheat is generally harvested in May and stem rust ordinarily comes too late to cause substantial damage. In the mountain regions, however, heavy losses are frequent in both winter and spring wheats.

West of Kwanhsien along the edge of Chengtu plain, in the mountains such as Chinchenshan and Panlanshan, *Berberis levis* Fr. (= *B. soulieana* Schn.) is one of the most common shrubs. It has been recorded at higher altitudes, up to 2,300 meters, but commonly it is found below 1,000 meters, mostly along creeks at the foot of the mountains. Early in April every year, the bright red infections of *Puccinia graminis* on the leaves (Fig. 1) are numerous and startling. The situation is equally as serious as, if not more so than, that of *B. vulgaris* L. in the north central United States. On Mount Omei, southwest of Chengtu plain, *Mahonia fortunei* is even more common than *B. levis*. Both species are usually severely infected by stem rust there. The *M. fortunei* appears to be restricted to the foot of the mountain, between 500 to 800 meters, and extends to the plain. *B. gagnepainii*, occurring from 1,500 meters to the summit of the mountain (3,100 meters), is less often rusted. Seven collections of the rust on *B. levis* and two collections on *M. fortunei* were incoulated to grain crops in 1940. The resulting good infection on wheat and barley but feeble infection on rye proved that all the collections belonged to *P. graminis tritici*. As a matter of fact, wheat and barley are the only small grains in the Chengtu plain infected naturally by stem rust, while oats and rye, the latter grown in the far north of Szechuan province and observed in experimental plots only, have never been seen infected. It is even more unlikely that all the common wild grasses in the Chengtu plain, such as *Poa*, *Agropyron*, *Agrostis*, *Sporobolus*, *Alopecurus*, *Elymus*, and *Bromus*, are also free from stem rust.

Northwestward, in the mountain ranges of Szechuan, covering Lifan, Maohsien, and Wenchuan, Dr. C. T. Wei observed in 1941 four species of *Berberis* common at levels around 2,000 meters, *i.e.*, *B. wilsonae* Hemsl., *B. silva-taroucana*, *B. verruculosa* Hemsl. et Wilson, and an undetermined species with round to broadly oval leaves. *B. wilsonae* has been seen very heavily rusted, *B. silva-taroucana* occasionally and lightly infected, while the other two species were free from rust.

In view of the common occurrence and the destructiveness of stem rust in many provinces in China, the role played by barberry deserves a thorough

and long study in order to solve the rust problem. The present note, based on limited observations, aims only to stimulate further investigations. It is a pleasure to acknowledge my indebtedness to Dr. C. T. Wei, Dr. C. S. Wang, and Dr. T. F. Yu for their cooperation in furnishing information and specimens.

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STUDIES IN THE FUSARIUM DAMPING–OFF OF CONIFERS. I. THE COMPARATIVE VIRULENCE OF CERTAIN FUSARIA[1, 2]

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INTRODUCTION

In the many reports of the relationship between Fusaria and damping-off in conifers, either observed or determined by inoculation experiments, the repeated occurrence of certain species suspected of being causal agents has led to the general acceptance of the pathogenic nature of a few of these. According to a compilation by Wollenweber and Reinking (32), of importance in Europe are *Fusarium oxysporum* v. *aurantiacum*, synonymous with *Fusoma parasiticum* Tubeuf (4, 29, 30, 31) and *Fusoma pini* Hartig (2, 9, 10), *F. oxysporum* v. *aurantiacum* f. 1 (*F. macroxysporum* Lindfors) (16), *F. bulbigenum* v. *blasticola* (*F. blasticola* Rostrup) (24), *F. culmorum*, *F. avenaceum* (*F. venenorum*) (6), *F. sambucinum*, *F. scirpi* v. *acuminatum*, *F. fuligenosum* and *F. echinosporum* (25), and *F. graminearum* (*Giberella saubinetii*) (19); and in the United States primarily *F. sporotrichioides*, *F. arthrosporioides*, *F. sambucinum* f. 6 (*F. discolor sulphureum* Schl.), and to a lesser extent *F. culmorum*, *F. solani*, *F. orthoceros*, *F. moniliforme*, *F. oxysporum*, *F. vasinfectum* and *F. graminearum* (12, 13, 20, 21, 26). These constitute only a small selection of the many species mentioned in the literature, and there is need for further tests with some of them as well as with other Fusaria, in order to determine which species are really parasitic and how they compare with other damping-off fungi used as standards. The object of the present investigation has been to carry out such tests by various critically studied experimental methods. Where more than one host was inoculated, relative susceptibility to infection was tested.

The effect upon the experimental design of limitations in time and space made it infeasible to consider damping-off losses according to the classical symptomatic categories (12, 13, 28): germination loss, normal or ordinary damping-off, root-rot or late damping-off, and top damping-off. Experiments were maintained long enough to test ability to induce normal damping-off, but probably not long enough to test potentialities of the Fusaria as root-rotting organisms. Damping-off losses were in two classes: (I) emergence loss, the reduction in the number of seedlings appearing above the surface of the substrate as compared with the total number of viable seeds, the latter determined by the emergence in uninoculated controls. This

[1] A portion of a dissertation presented to the faculty of the Graduate School of the University of Pennsylvania in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

[2] The writer wishes to express appreciation to: Dr. H. H. York under whose direction the investigation was carried out; Dr. W. G. Hutchinson for criticism of the manuscript; Dr. P. V. Lufkin for assistance on statistical analysis; and Dr. C. D. Sherbakoff for identifications of some Fusaria used in the investigations.

[3] The greater part of this investigation was carried on during the tenure of a George Leib Harrison Fellowship at the University of Pennsylvania.

TABLE 1.—*Identity and sources of fungi tested for ability to cause damping-off of coniferous seedlings*

Species[a]	Line	Host source	Year of isolation	Locality	Isolator[b]
Fusarium aquaeductuum (Radlk. & Rabh.) Lagh. v. *medium* Wr.	1C[c]	Red pine (discolored wood of stem, 16-yr.-old tree)	1932	Hemlock Lake, N. Y.	Y
F. arthrosporioides Sherb.	52	Scotch pine (damping-off)	1940	Washington Crossing, N. J.	T
F. avenaceum (Fr.) Sacc.	51[c]	" " " "	"	" " " "	T
	59[c]	" " " "	"	" " " "	T
	64[c]	" " " "	"	" " " "	T
	66	" " " "	"	" " " "	T
	69[c]	" " " "	"	" " " "	T
F. equiseti (Cda.) Sacc.	27	White pine (damping-off)	"	Philadelphia, Pa.	K
F. graminearum Schwabe	50	Scotch pine (damping-off)	"	Washington Crossing, N. J.	T
F. javanicum Koord. v. *radicicola* Wr.	R32	American Type Culture Coll.	.....	.....	.....
F. moniliforme Sheld.	R35	" " " "	.....	.....	.....
F. orthoceros App. & Wr.	16[c]	White pine (discolored wood of root)	1937	Hemlock Lake, N. Y.	Y
	R23A[c]	Red pine (root rot, 1–2-yr.-old seedlings)	1939	Saratoga Springs, N. Y.	E
	28[c]	White pine (damping-off)	1940	Philadelphia, Pa.	K
F. orthoceros App. & Wr. v. *longius* (Sherb.) Wr.	R60	Scotch pine (damping-off)	"	Washington Crossing, N. J.	T
	61	" " " "	"	" " " "	T
F. oxysporum Schl.	30	American Type Culture Coll.	.....	.....	.....
F. poae (Peck) Wr.	R11C[c]	Red pine (extra-seasonal growth (15), in 1935 node)	1936	Hemlock Lake, N. Y.	Y
	68[c]	Scotch pine (damping-off)	1940	Washington Crossing, N. J.	T

TABLE 1.—(*Continued*)

Species[a]	Line	Host source	Year of isolation	Locality	Isolator[b]
F. reticulatum Mont.	26A	White pine (damping-off)	1940	Philadelphia, Pa.	K
	58[c]	Scotch pine (damping-off)	"	Washington Crossing, N. J.	T
	62	" " " "	"	" " " "	T
F. sambucinum Fuckel	R8A[c]	Norway spruce (wood 1-in. root of 26-yr.-old tree)	1937	Hemlock Lake, N. Y.	Y
F. scirpi Lamb. & Fautr. v. *acuminatum* (Ell. & Ev.) Wr.	R22[c]	Red pine (stem wood of 1925 node)	1931	" " " "	Y
F. solani (Mart.) App. & Wr.	R9B[c]	White pine (inner bark of root crown)	1932	Norwich, N. Y.	Y
F. solani (Mart.) v. *Martii* (App. & Wr.) f. 1 Wr.	R2A[c]	White pine (wood of $\frac{1}{8}$-in. root of 22-yr.-old tree)	1936	" " "	Y
F. solani (Mart.) App. & Wr. v. *minus* Wr.	67	Scotch pine (damping-off)	1940	Washington Crossing, N. J.	T
F. sporotrichioides Sherb.	R33	American Type Culture Coll.	.....	.....	.....
F. vasinfectum Atk.	R34	" " " "	.....	.....	.....
Penicillium sp.	CI	Greenhouse soil	1940	Philadelphia, Pa.	T
Pythium ultimum Trow.	1145	Douglas fir (damping-off)	1925	Monument, Colorado	J
Rhizoctonia solani Kühn	631	Tulip poplar (collar rot)	.....	.....	J
Sclerotium bataticola Taub.	573	Red pine (collar lesion)	.....	Frederick Jc., Maryland	J

[a] Nomenclature after Wollenweber and Reinking (32).

[b] Isolations by: Y, Dr. H. H. York, Department of Botany, University of Penna.; E, E. J. Eliason, State Department of Conservation, Saratoga Springs, N. Y.; K, P. D. Keener, Dept. of Botany, University of Penna.; T, the writer; J, L. W. R. Jackson, B.P.I.S. & A.E., U. S. Dept. of Agriculture.

[c] Identified by C. D. Sherbakoff, Univ. of Tenn. Agricultural Experiment Station.

class thus included the decay of seed as well as the early rotting of radicles. (II) Post-emergence damping-off, the reduction of the total number of emerged seedlings through normal damping-off, top damping-off and root rot, all cases of infection being tabulated only if fatal before the termination of the experiment. The two categories could then be summarized in a survival count, based upon the number of seed planted, which, when contrasted with an uninoculated control, would provide a measure of the whole effect of the damping-off organism for the duration of the experiment.

MATERIALS AND METHODS

Isolations were made by dipping infected portions of diseased plants in four per cent formalin for two minutes and then placing them without rinsing upon two per cent agar without nutrients. A modification of this method was used with the fungi which were secured under conditions of pure saprophytism or whose origins were not known. Surface sterilized seeds of *Pinus resinosa* Ait. were sown on agar cultures of such fungi and then isolations were made from seedlings which damped-off after germination. With this method each fungus invariably produced a certain amount of injury, as demonstrated either by the decay of radicles or normal damping-off. Passing fungi of unknown pathogenicity through a potential host permitted the selection of more virulent strains, which could then be compared with other fungi isolated from authentic cases of the disease.

Monosporous transfers were made with a micromanipulator. Every monosporous culture coming from diseased seedlings, either directly by isolation or indirectly from passage through a host, is called a line throughout this paper. Stock cultures were maintained on potato-dextrose agar (Difco, pH 5.6) in cold storage at 8° to 10° C. or at room temperature from 18° to 25° C. A list of the names and sources of the fungi tested is given in table 1.

The selection of hosts for pathogenicity tests was based upon a compilation of susceptible conifers listed by Hartley (12). The list was restricted to abietinean conifers owing to their economic significance in reforestation and to the frequency of reports of disease among them. All seeds were kept in dry, unsealed containers in a cold-storage room at 8° to 10° C. A list of the species in the various inoculation tests is given in table 2.

Inoculations were made in liquid, quartz-sand, and autoclaved-soil cultures. All seeds, before planting, were surface-sterilized by immersion for 3 minutes in an aqueous solution of 0.1 per cent bichloride of mercury, followed by at least 5 rinses in sterilized distilled water.

Inoculum was prepared by growing the fungus on a substrate of 25 cc. of polished rice grains in 35 cc. of distilled water autoclaved for 20 minutes at 15 pounds' steam pressure. This sterile rice-mush was thoroughly permeated by the average *Fusarium* in 3 weeks at 28° C. Unless otherwise indicated, the inoculum was added to the substrate upon which the hosts were to be grown, at the approximate rate of one cubic centimeter per 5 square inches of surface. After the inoculum was mixed with the upper

inch of substrate, this entire layer was removed, thoroughly mixed in a mortar and replaced upon the surface of the pot or flat. This provided for uniform distribution of the inoculum in the upper inch of substrate, as well as for uniformity of age and quantity of inoculum of the different fungi. In the case of the liquid cultures, however, it was necessary only to add to the substrate a single hyphae-permeated rice grain of inoculum.

For those experiments in which liquid or quartz-sand media were used, a nutrient solution was selected which would be stable under emendation for pH and nutrition study and, at the same time, adequate for the growth of both hosts and pathogens. Glycerinated phosphates met these requirements. The advantages of substituting a salt of glycerophosphoric acid for that of phosphoric in standard nutrient solutions have been described (1). The solution ultimately adopted was a modification of a glycerophos-

TABLE 2.—*Seed source of conifers used in damping-off trials*

Species[a]	Year of collection	Locality of collection[b]
Pinus resinosa Ait.	1932	Adirondack region, N. Y. (a)
Pinus sylvestris L.	1938	Brushton CCC Camp, N. Y. (a)
Abies concolor Lindl. & Gord.	1940	San Isabel Forest area, Colorado (b)
Pinus nigra Arnold v. *austriaca* Aschers & Graebn.	1940	Illinois (b)
Picea pungens Engelm.	1940	San Isabel Forest area, Colorado (b)
Pinus ponderosa Dougl.	1940	Lewis and Clark N. F. Mont. (c) (4000 ft., kiln extracted)
Pinus banksiana Lamb.	1937–38	Superior, N. F., Minn. (c)
Pseudotsuga taxifolia Brit.	1939	Mt. Baker Forest, Darrington, Wash. (c)

[a] Taxonomy of conifers after Rehder (22).
[b] Seed received from: (a) E. J. Eliason, State Tree Nursery, New York State Conservation Department, Saratoga Springs, N. Y.; (b) Herbst Bros., New York City; (c) H. L. Shirley, Allegheny Forest Experiment Station, Phila., Pa.

phate type successfully used by Jackson (14) for the growth of Douglas Fir and *Pinus ponderosa*, as well as various isolates of *Pythium* and *Rhizoctonia*. The concentrations of the constituent salts were as follows: calcium nitrate, 0.007 M; magnesium sulphate, 0.04 M; sodium glycerophosphate, 0.04 M; potassium chloride, 0.01 M; iron citrate, to yield approximately 2 ppm. (1 ml. 1 per cent solution); boron (boric acid), 0.05 ppm.; copper (sulphate), 0.02 ppm.; manganese (chloride), 0.5 ppm.; and zinc (chloride), 0.05 ppm. The salts were made up in stock solutions, sterilized by autoclaving, and added to distilled water in the proper quantities to make the required concentrations as needed. The reactions of the solutions were adjusted to desired endpoints with 0.1 N HCl and 0.1 N NaOH. All pH determinations were made potentiometrically with quinhydrone and saturated calomel half-cells.

INOCULATION EXPERIMENTS AND RESULTS

Liquid Cultures

In preliminary tests, *Pinus resinosa* grown upon sterile liquid medium in test tubes was inoculated with a number of fungus lines (Fig. 1), following

with some modification the technique described by van Luijk (17) for grasses and applied to conifer study by Ten Houten (28). A hollow cylinder of filter paper, with the upper end covered by a lid bearing six 2-mm. holes

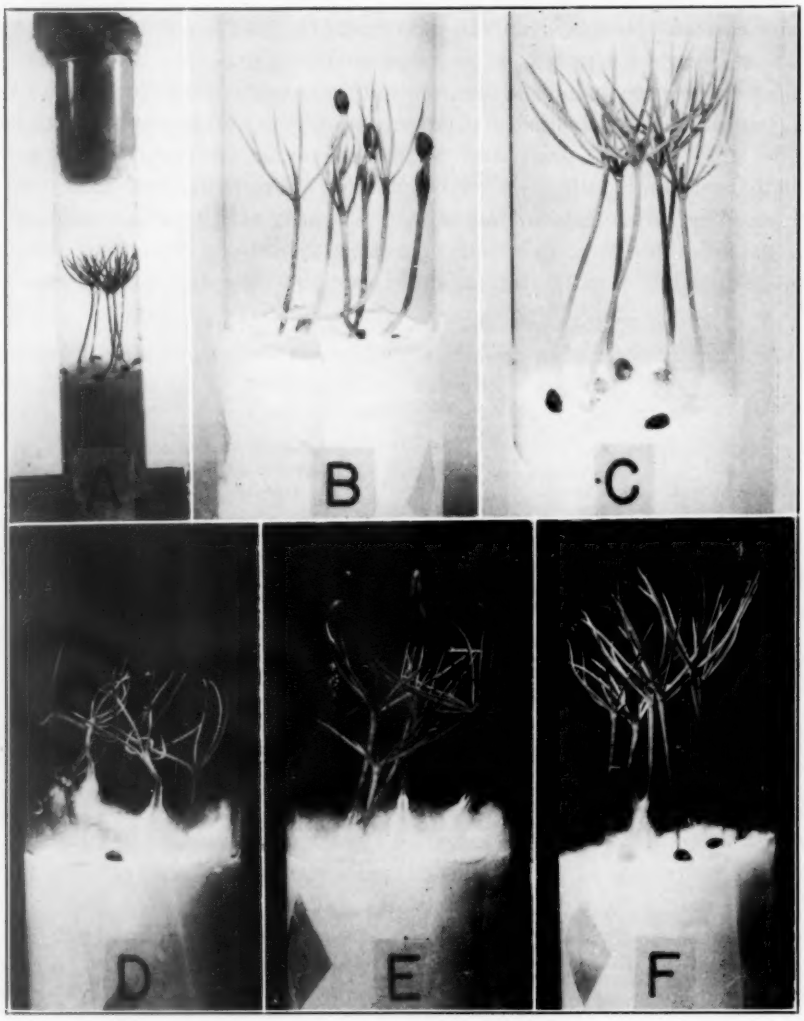

FIG. 1. Inoculation of seedlings of *Pinus resinosa* with lines of *Fusarium* in sterile liquid medium.

Control series: A. View of entire culture tube showing arrangement of seedlings. B. Enlarged view of sterile seedlings, 8 days after transplanting. C. Sterile seedlings 30 days after transplanting.

Inoculated series at termination of experiment (21 days). D. *Fusarium orthoceros* v. *longius* (R60), all seedlings attacked. E. *F. moniliforme* (R35), all attacked. F. *F. vasinfectum* (R34), 3 seedlings to right not attacked and without typical constrictions.

regularly distributed along the periphery and a larger aperture (5 mm.) in the center, was inserted into the bottom of a test tube (3.5 × 20 cm.). Exactly 50 cc. of nutrient solution, adjusted to yield pH 6 after sterilization,

was added so that the surface of the liquid reached the level of the lid. The tube was then plugged and autoclaved. Seedlings from surface-sterilized seed, germinated in sterile agar and closely checked for sterility after germination and with radicles from one to three cm. long, were transplanted to the tubes with aseptic precautions. The radicle of a seedling was inserted through one of the peripheral holes in the lid of the cylinder. The cultures were placed in a greenhouse (thermostatic control, 68°–75° F.) for three days. Seedlings that failed to grow were removed and replaced. When all seedlings were growing satisfactorily, the tube was inoculated by inserting a grain of inoculum into the liquid through the central hole in the lid. A small quantity of glass wool within the cylinder served to lodge the inoculum

TABLE 3.—*Damping-off of Pinus resinosa seedlings inoculated with various fungi in liquid cultures*

Line no.	Fungus	Number of seedlings inoculated[a]	Number of seedlings invaded	
			After 10 days	After 21 days
R11C	*Fusarium poae*	12	12	12
R34	*F. vasinfectum*	18	10	14
R33	*F. sporotrichioides*	36	27	35
R60	*F. orthoceros* v. *longius*	18	12	18
16	*F. orthoceros*	18	17	18
64	*F. avenaceum*	12	12	12
R32	*F. javanicum v. radicicola*	18	6	9
58	*F. reticulatum*	12	12	12
1C	*F. aquaeductuum* v. *medium*	12	3	7
R8A	*F. sambucinum*	18	5	7
R35	*F. moniliforme*	18	11	18
R2A	*F. solani* v. *martii* f. 1	12	3	8
631	*Rhizoctonia solani*	12	12	12
Control		24[b]	0	0

[a] Six seedlings per tube.
[b] An additional control tube showed a mold several days after the seedlings were transplanted. Two seedlings were rotted at the expiration of the test (21 days).

just below the surface of the liquid, as well as to provide support for the seedlings. Holes cut in the sides of the cylinder permitted the observation of the development of the host and the fungus. The inoculated tubes were kept for 3 weeks in the greenhouse.

The criterion of whether a fungus was able to attack the host was the visible evidence of a constriction in the root or hypocotyl, where the cortical tissue was destroyed. A collapse of the seedling, the typical normal damping-off symptom, could not always be used because the seedling received considerable support from adjacent plants and from the wall of the tube; nor could fungal growth along aerial portions of the plant be used as a sign of infection, since this commonly occurred because of high humidity. However, from seedlings with typical constrictions (Fig. 1, D, E and F), surface-sterilized and sown on potato-dextrose agar, the inoculated fungus could be isolated. Plates from unconstricted seedlings, with the same treatment, invariably remained sterile.

All 12 of the Fusaria in the liquid-culture inoculation tests were pathogenic (Table 3). *Fusarium avenaceum, F. poae, F. moniliforme, F. reticulatum* and the two varieties of *F. orthoceros* caused complete losses, comparing thus in virulence with the Rhizoctonia line. *F. sporotrichioides* was also highly parasitic. The rest of the lines were moderately parasitic. *F. sambucinum* was the least virulent of the lines tested in this experiment.

Quartz-Sand Cultures

The quartz-sand cultures (Fig. 2) were maintained in four-inch pots with sand that had been washed for several hours in cold, running water, soaked in hot water, and then rinsed in distilled water. Each pot was painted on all surfaces with DuPont acid- and alkali-resistant black paint to

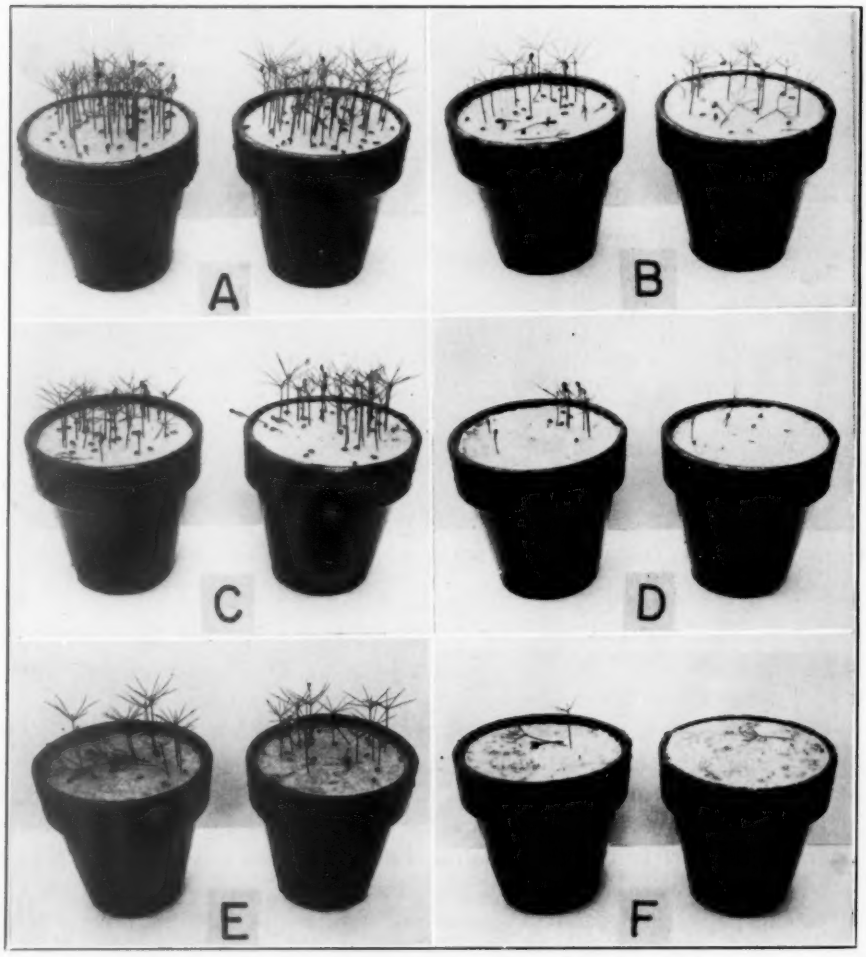

FIG. 2. Inoculations in quartz-sand cultures of *Pinus resinosa* with lines of *Fusarium*, photographed 26 days after planting and 14 days after emergence: A. Controls. B. *F. orthoceros* v. *longius* (Line 61). C. *F. poae* (Line 68). D. *F. reticulatum* (Line 58). E. *F. oxysporum* (Line 30). F. *F. avenaceum* (Line 66).

reduce water loss through evaporation. The pots of sand were covered with Petri-dish lids and autoclaved for one hour at 15 pounds. After inoculation, the pots were flooded with the standard nutrient solution adjusted to pH 6. and were incubated at room temperature for several days to permit thorough permeation of the sand by the fungi. Each line was inoculated in duplicate and controls were prepared with sterile rice-mush. Fifty surface-sterilized

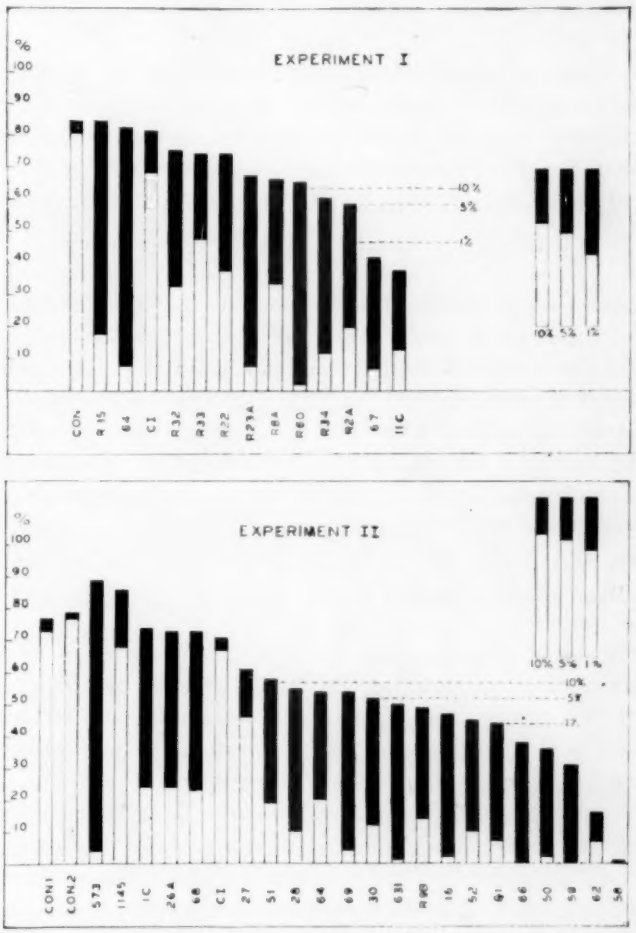

FIG. 3. Diagram showing the results of inoculations of quartz-sand cultures of *Pinus resinosa* with various fungi: comparative emergence (length of bar), post-emergence damping-off (black) and final stand (white). Levels of significance for emergence (dashed lines) and post-emergence losses (black portions of bars to right) are given.

seeds of *Pinus resinosa* were then sown on the surface of each pot and covered with one-quarter inch of sterile sand. The pots were kept in the greenhouse and watered daily by flooding with nutrient solution freshly prepared by adding sterile stocks to distilled water, without autoclaving. The glass covers were removed after the seedlings began to emerge from the sand.

All the fungus lines were tested in two experiments, and although the

first was started two weeks before the second, each was maintained for three months under identical greenhouse conditions. The seedlings which damped-off after emergence were removed as soon as recognized and the numbers recorded. The results are in figure 3. The error variance, or the differences in results derived from each of a pair of duplicate pots in a treatment, was statistically employed for determining the significance of the variance between lines and between each line and the control used as a standard (18, 23).

A certain amount of post-emergence loss was evident in all the control series, although relatively small. This was unavoidable, since no precautions were taken to prevent contaminations by air-borne organisms, and in the duration of the experiment some managed to enter the controls. Fusaria were isolated less than once out of eight times from control seedlings which damped off.

Sterilized-Soil Cultures

Inoculation tests in soil were performed on all the coniferous hosts with a selection of Fusarium lines and the fungi used as standards (Fig. 4). The soil contained three parts of loam, two of sand, and two of leaf-mold. After steam sterilization the final pH was 5.8. The soil was placed in wooden flats, with inside dimensions of $9 \times 12 \times 5$ inches and each was autoclaved for one hour at 15 pounds pressure on two successive days. Following sterilization, heavy paper covers reduced air contamination until seedlings began to emerge, after which the covers were removed. Flats were inoculated, and controls were prepared, as were pots for the sand-culture experiments. The general thinning of stands (Fig. 4), as compared with the control, indicated a uniform distribution of inoculum.

Three rows of 50 or 60 seeds of each host, depending upon the relative size of the seed, were sown in each flat, making the density of sowing in soil comparable with that in the sand experiments. Each flat was watered daily by top-irrigation with distilled water. The tests were maintained for four months in the greenhouse (daily mean temperature, 68–80° F.), after which the surviving seedlings were removed, the flats resterilized and the entire set of inoculations repeated. Thus the duplicate set in this case was not run concurrently. However, the greenhouse conditions under which both sets were maintained, the first in the spring and early summer and the second in the fall of that year, were made as closely alike as possible and there was no variation in the standard inoculation and planting procedures. The results of the inoculations are given quantitatively in figure 5, each percentage value being the average of the two trials. Some damping-off again occurred in the controls, but as in previous experiments, only a relatively small percentage of the isolations from these seedlings yielded Fusarium species. The losses caused by this accidental contamination were extremely small and insignificant in comparison with those in the inoculated flats.

No attempt was made to evaluate the virulence of the various fungi on the basis of a consideration of each host-fungus combination. As is evident

from the results, most of the lines showed variability in virulence within themselves on the different conifers. Some lines were fairly consistent: for instance, *Fusarium poae* (Line 11C) and *F. reticulatum* (Line 58) repeatedly reduced emergence of all the hosts to 10 per cent or less of seed sown;

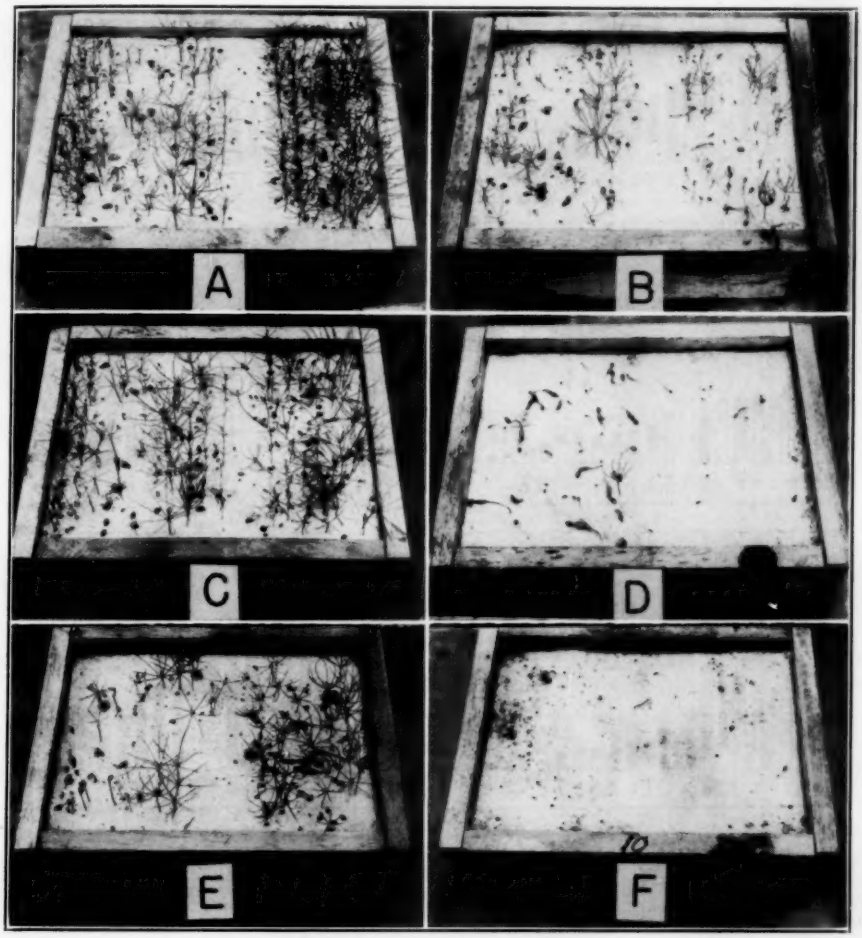

FIG. 4. Inoculations in autoclaved-soil cultures of coniferous hosts with various fungus lines. Hosts arranged in groups of three rows, left to right: *Pinus resinosa, Abies concolor, Picea pungens, Pinus ponderosa, Pinus banksiana,* blank (originally planted with seeds of *Pinus strobus* L. but seeds germinated too late and in too few numbers to be comparable with other hosts), *Pinus sylvestris, Pseudotsuga taxifolia* and *Pinus nigra austriaca.* A. Control, 28 days after planting. B. *F. equiseti* (Line 27), 22 days. C. *Sclerotium bataticola* (Line 573), 28 days. D. *F. avenaceum* (Line 66), 20 days. E. *F. orthoceros* (Line 23A), 26 days. F. *F. reticulatum* (Line 58), 23 days.

while *F. avenaceum* caused severe or complete post-emergence losses of all the hosts. Another means of analyzing the data was to consider the pathogenicity of each fungus on all the hosts simultaneously, expressed in terms of the mean emergence or mean post-emergence damping-off that each caused

on all the conifers. Conversely, from the same data, it was possible to measure the relative susceptibility of each host to all the fungi and express it as

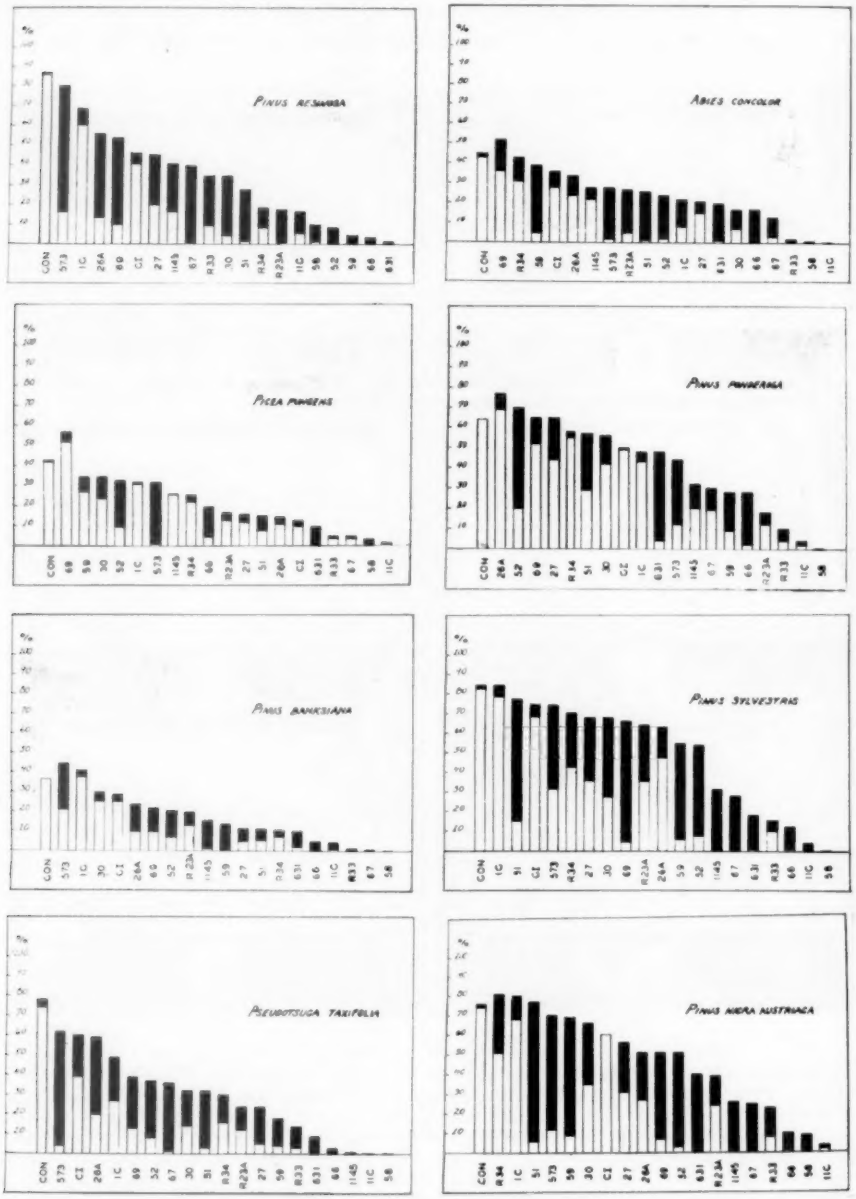

FIG. 5. Diagram showing results of inoculations with various fungi in sterilized-soil cultures of conifers: emergence (Length of bar); post-emergence damping-off (black); final stand in percentage of seed (white).

a mean value. The significance of the differences between such means was determined by analyses of variance, subdividing the variance into three

TABLE 4.—*Total percentage emergence of all hosts in autoclaved-soil cultures inoculated with various fungus lines*

Fungus line	Average percentage emergence of all hosts for each fungus line		Order of ability to reduce emergence
	Actual means	Means based upon controls evaluated at 100 per cent	
58	2.9	4.2	1
11C	4.1	6.2	1
R33	13.2	17.6	2
66	12.4	22.3	3
67	22.2	31.2	4
631	19.6	32.4	4
1145	24.9	41.7	5
R23A	28.3	45.2	6
27	35.7	53.1	7
59	32.6	53.7	7
52	40.3	59.9	8
R34	42.0	65.9	9
30	42.2	67.5	9
CI	46.0	69.9	10
26A	47.5	72.1	11
1C	53.1	82.8	12
69	50.7	83.5	12
573	54.4	84.8	12
Con	64.2	100.0	.....
Least significant difference between means	1.3	2.2	.....

portions: among fungi, among hosts, and between duplicate series of tests (18, 23).

These analyses revealed extremely high variability among fungi and among hosts. In considering emergence data, a slight significance was apparent in the variance due to duplication; however, upon evaluating the emergence in the controls for each series at 100 per cent and reanalyzing the emergence in the inoculated flats in terms of percentage of control, the significance for duplicate trials disappeared. Thus the general effects of the

TABLE 5.—*Total percentage emergence of each host in autoclaved-soil cultures inoculated with various fungus lines*

Host	Average percentage emergence of hosts for fungus lines		Order of susceptibility to emergence loss by Fusaria
	All lines	Fusarium lines	
Pinus resinosa	36.5	33.3	1
Pseudotsuga taxifolia	35.9	34.4	1–2
Pinus banksiana	44.5	38.3	2
Picea pungens	48.2	48.6	3
Abies concolor	53.0	50.6	3
Pinus sylvestris	57.4	56.8	4
P. nigra austriaca	61.7	60.8	4–5
P. ponderosa	63.9	62.9	5
Least significant difference between means of all lines	4.6		

TABLE 6.—*Total percentage post-emergence damping-off of all hosts in autoclaved-soil cultures inoculated with various fungus lines*

Fungus line	Average percentage post-emergence loss of all hosts for each fungus line	Order of ability to cause post-emergence loss
631	95.8	1
66	94.0	1
52	83.8	2
67	82.4	2
573	78.2	3
59	77.6	3
51	76.4	3
R33	64.2	4
1145	58.5	5
69	55.9	5–6
R23A	52.8	6–7
30	50.5	7
27	44.8	8
26A	39.9	9
R34	34.4	10
1C	21.6	11
CI	13.5	12
Con	2.2	.....
Least significant difference between means	3.7	

fungi in the two trials were fundamentally alike; the general emergence potential differed, a condition probably arising from unavoidable variations in the extremely critical sterilization treatment of the seeds. The assumption of optimum germination in the controls permitted a comparison of host reactions to the fungi apart from the different capacities of the seed for germination.

On the basis of these analyses, the results of the soil-culture experiments could be arranged in orderly sequences. The average percentages of emergence of all the hosts for each fungus treatment are given in table 4 in order of increasing sprouting, and the actual means as well as those based on con-

TABLE 7.—*Total percentage post-emergence damping-off of each host in autoclaved-soil cultures inoculated with various fungus lines*

Host	Average percentage post-emergence loss of hosts for fungus lines		Order of susceptibility to post-emergence loss by Fusaria
	All lines	Fusarium lines	
Pinus resinosa	65.8	75.9	1
Pseudotsuga taxifolia	69.9	73.4	1
Pinus nigra austriaca	62.8	65.2	2
Abies concolor	59.4	65.1	2
Pinus sylvestris	57.0	58.6	3
P. banksiana	51.1	52.3	4
P. ponderosa	39.7	39.1	5
Picea pungens	35.7	31.5	6
Least significant difference between means of all lines	5.6		

trols equal to 100 per cent emergence are included. In addition, the lines are ranked on the basis of their ability to reduce emergence. In table 5 is a like arrangement of hosts, based upon the average emergence after inoculations with all fungus lines, and with Fusarium lines alone. The hosts were ranked in order of susceptibility to emergence loss from the Fusaria. Similar rankings with respect to post-emergence losses are in tables 6 and 7.

DISCUSSION

The results of these inoculation experiments with various lines of fungi, predominately Fusaria of parasitic and saprophytic origin, on a general coniferous population, indicated that certain species of Fusarium were capable of causing extreme reductions in emergence of the total viable seeds of the hosts (Figs. 3 and 5). In some cases the losses were greater than those caused by the standard lines of *Rhizoctonia*, *Sclerotium*, and *Pythium*. Furthermore, some Fusarium lines were comparable with these standards in their ability to cause post-emergence damping-off. In the two sand-culture experiments, 15 of 29 different Fusarium lines tested, significantly reduced emergence in comparison with the respective control series, and 8 of these were beyond the 1 per cent level of probability. Three additional lines produced reductions of questionable significance. All the lines save *F. equiseti* caused significant post-emergence losses, the exception occurring within the doubtful probability level. Of the standard lines, a common mold, *Penicillium* sp., and the *Pythium* line, in both experiments neither reduced emergence nor caused significant post-emergence loss. *Sclerotium bataticola* produced no emergence loss but did cause a high percentage of post-emergence damping-off, and *Rhizoctonia solani* was highly virulent both before and after seedling emergence.

Different isolates within the species *Fusarium orthoceros*, *F. reticulatum*, *F. avenaceum*, and *F. poae*, varied in ability to cause emergence losses in conifer seedlings.

In the soil experiments all the lines tested significantly reduced emergence of the hosts when compared with uninfected controls. Five lines of *Fusarium* caused greater emergence losses than did the lines of *Rhizoctonia* or *Pythium*. Six additional Fusaria ranged in virulence from a degree comparable with these standards to one resembling the *Penicillium*. *Sclerotium bataticola* reduced emergence the least of all the lines tested. All lines caused significant post-emergence losses when compared with the control. *Rhizoctonia solani* and *Fusarium avenaceum* caused the greatest losses. From the high rate of mortality of the few seedlings which germinated in inoculations with *Fusarium poae* (Line R11C) and *F. reticulatum* (Line 58), these lines appeared capable of inducing post-emergence losses comparable with emergence losses; however, for reasons already stated, these were omitted from the analysis. Three Fusarium lines were more virulent than the *Sclerotium*, and six were more virulent than the *Pythium*. *F. aquaeductuum* v. *medium* caused the least damage of the Fusaria, and the Penicillium less than any of the lines.

Failures of emergence in coniferous nursery beds have long been associated with damping-off organisms; however, species of *Fusarium* on the whole have generally been credited with less ability to cause pre-emergence than post-emergence losses (11, 12, 13, 28). Results of the present experiments indicate relatively equal virulence for Fusaria in both aspects of this disease, and agree with other observations (8, 21) that many Fusaria may reduce sprouting by the early decay of radicles. One author has stated that *Pythium ultimum* and virulent strains of *Corticium* (*Rhizoctonia*) *solani* apparently caused more germination losses of conifers than any Fusarium line tested, with the exception of *F. sporotrichioides* (21). The present investigations in soil and sand substrates, particularly the latter, indicate to the contrary that a number of Fusarium lines may reduce emergence to a greater extent than the species mentioned.

Rather high emergence losses and post-emergence losses consistently resulted from inoculations with *Fusarium reticulatum* (Line 58), *F. poae* (Line R11C), *F. avenaceum* and *F. sporotrichioides;* moderate losses of both types followed inoculations with *F. vasinfectum* and *F. oxysporum;* but *F. aquaeductuum* v. *medium* caused little loss of either kind. Other lines were less consistent: some caused considerable emergence reduction with relatively little subsequent attack; others reduced emergence comparatively little, but caused high post-emergence losses.

The virulence of the fungi depended to a very large extent upon the conditions under which they were tested. In liquid culture inoculations in test tubes, where only post-emergence attack was considered, all the lines caused appreciable or complete destruction of seedlings, even the relatively nonvirulent Line 1C. The conditions set up favored the fungus to such extent that even the least virulent organism attacked the host in the unnatural environment. Fine distinctions of relative virulence are not obtained by this method. In quartz-sand cultures, where the host had a solid substrate, approximately half the lines significantly reduced emergence while almost all caused heavy post-emergence losses. Here again conditions favored the fungi to the extent that the severity of most of the losses permitted little comparison of relative virulence of the fungi.

The soil-culture method, wherein most of the lines caused both types of loss, represents the closest approach in the laboratory to a duplication of nursery conditions. However, some artificiality is again evident, particularly in the sterilization of the soil, a procedure which is essential in order to remove potential damping-off organisms or any others that might affect the activity of the test organism, but which, as shown by Lindfors (16), unquestionably increases the severity of Fusarium attack. The generally greater emergence in the sand cultures compared to that in soil could not be explained as inability of the fungus to thrive in the sand, since sufficient rice-mush was carried along and uniformly distributed with the fungus mycelium in the process of inoculation so that ample nutrition was afforded the fungi. In addition, the fungi received accessory nutrient material in

the sand cultures from the standard nutrient solutions supplied. The poorer retention of moisture by the coarse particles of sand, with consequently better aeration, probably stimulated emergence and allowed the fungi less opportunity to act upon radicles. These results paralleled Spaulding's observation (27) that the use of a coarse sand cover apparently increased resistance to the disease.

The simultaneous inoculation of all hosts as in the sterilized-soil tests, permitted a valid comparison of their relative susceptibility to Fusaria. Emergence and post-emergence losses were greatest in *Pinus resinosa* and *Pseudotsuga taxifolia*. Hartley's (12) observations have indicated, somewhat differently, that *Pinus resinosa* is more susceptible to the later forms of damping-off than to germination losses. However, from his compilation of the literature on relative susceptibility of conifers, there is general agreement with the present results for *P. resinosa,* most of the reports indicating a relatively high degree of susceptibility to damping-off. *Pseudotsuga taxifolia* frequently has been reported as somewhat less susceptible, although later work (5) describes severe attacks on this species. Rathbun-Gravatt (21) had comparable results on *P. resinosa* and *P. banksiana,* the seeds of the former showing reduced germination percentages in the presence of Fusarium, a result compatible with those of the present investigation. *P. banksiana* proved somewhat less susceptible to post-emergence losses. *Abies concolor* was of moderate relative susceptibility to both categories of losses, somewhat at variance with early reports of its extremely high susceptibility to damping-off (3, 4). Hartley (12) states that literature reports indicate relative susceptibility of *Pinus ponderosa* and resistance of *Picea pungens.* The present results agree with the latter observation. *P. pungens,* although moderately attacked before emergence, suffered the least post-emergence loss of the conifers tested. *Pinus sylvestris* has variously been reported as ranging from less susceptible than average to most susceptible (12). The present tests have indicated its relatively intermediate response to both types of attack.

In all these experiments, the virulence of the fungi probably depended to a considerable extent upon the nature of their nutrition prior to inoculation. Fusaria grown upon rice decoction have been more virulent than the same organisms from nutrient agars (20, 28). This is probably due to a higher production by the fungus of toxic materials on the rice, as suggested by the investigations of Ten Houten (28) and of van Eek (7), who is cited by the former to have secured a stronger attack with the extract of a Fusarium culture on rice than with the living fungus itself. Hence, in all the experimental methods used in these studies, the employment of moderately heavy, toxic inoculum, dense sowing, abundant moisture, and greenhouse conditions unquestionably favored the development of the fungi to an extent far exceeding that which would normally be encountered in the field; and probably the magnitude of the losses seen in the tests would ordinarily not

be met in the nursery. However, the possibility remains that under some circumstances, conditions might become similarly favorable for the establishment of comparable host-pathogen relationships. Thus species of *Fusarium*, normal saprophytes in the nursery, might suddenly become highly virulent.

SUMMARY

Four fungi used as standards and monosporous cultures of twenty-five Fusarium lines, some parasitic and others saprophytic, were tested for ability to cause damping-off of coniferous species. A method of host-passage to determine pathogenicity is described. Eight coniferous hosts were selected for inoculation tests.

Losses are tabulated as: (I) emergence loss, including seed decay and destruction of radicles before emergence of seedlings from the substrate; and (II) post-emergence loss, including normal damping-off, top damping-off, and all root-rot fatal before the termination of the experiment.

The relative values of some standard inoculation procedures for testing relative virulence is discussed.

In liquid-culture inoculation tests in glass tubes, of twelve lines of *Fusarium* tested on seedlings of *Pinus resinosa*, six caused complete loss, comparing in virulence with a standard line of *Rhizoctonia solani*.

All of the lines were tested in quartz-sand cultures of *Pinus resinosa* seedlings. Approximately half of the Fusaria reduced emergence significantly compared with the uninfected control, and all save one caused heavy post-emergence losses, the significance of the exception being questionable. Of the standard lines: *Sclerotium bataticola* did not lower emergence but caused high post-emergence losses; *Rhizoctonia solani* effected severe losses in both categories; and *Pythium ultimum* and *Penicillium* sp. did not significantly reduce emergence or cause post-emergence losses.

Inoculation tests in sterilized-soil culture gave the most statistically reliable results of the methods employed because of the higher degree of replication available for analysis. The relative virulence of fifteen Fusarium lines and four standard cultures for a general coniferous population, represented by the eight hosts, was determined; and conversely, the range of susceptibility of the hosts to the entire group of damping-off fungi was ascertained. A number of the Fusarium lines equalled and occasionally exceeded in virulence the cultures of *Pythium* and *Rhizoctonia*, causing reduced emergence and increased post-emergence losses. *Sclerotium bataticola* caused the least emergence loss but post-emergence attack was relatively high. *Pinus resinosa* and *Pseudotsuga taxifolia* were equally most susceptible to both phases of the disease. *Pinus ponderosa* had the least emergence loss and *Picea pungens* the least post-emergence loss.

Nursery losses due to these fungi could be expected to be less severe than those thus experimentally induced; however, conditions under some circumstances might resemble those in the tests, in which event losses of similar

magnitude caused by normally saprophytic or moderately parasitic species of *Fusarium* could be expected.

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STUDIES IN THE FUSARIUM DAMPING-OFF OF CONIFERS. II. RELATION OF AGE OF HOST, pH, AND SOME NUTRITIONAL FACTORS TO THE PATHOGENICITY OF FUSARIUM[1]

HOWARD TINT[2,3]

(Accepted for publication January 15, 1945)

The damping-off diseases of coniferous seedlings are usually epidemic in character. Their economic significance is due to the irregularity of the losses as well as to the severe reductions in nursery stands. In a single nursery, in one season, damage may be negligible or moderate; whereas, in the next growing period, losses may be severe. Adjacent seed beds may be attacked in highly varying degrees. Obviously, certain predisposing factors must operate, singly or in a particular combination, at any given time, to account for the variability in losses.

Under certain conditions many species of *Fusarium* cause severe reductions in emergence as well as high post-emergent mortality (36). The present investigation deals with variations in environmental conditions affecting this host-pathogen relationship.

GENERAL MATERIALS AND METHODS

The selection of hosts and damping-off fungi was based upon results from a previous experiment (36). The sources of seeds and of the Fusarium lines were described in detail, as well as standard methods of seed sterilization, selection of monosporous cultures of virulent strains of fungi, preparation of inoculum and glycerophosphate nutrient solutions for the hosts and fungi. A division of the damping-off losses into two categories, emergence loss and post-emergence damping-off has been described. The same division was followed in evaluating losses due to inoculations with fungi in the following tests. Where experimental procedure required occasional departures from these standard methods, the alternative treatments are described.

All seedlings were grown in a low-humidity greenhouse, thermostatically adjusted to maintain a daily mean temperature range of 68–75° F., in those seasons of the year when such control was possible.

Determinations of pH were made potentiometrically with quinhydrone and saturated calomel half-cells, and all solutions were adjusted in acidity with 0.1 N HCl and 0.1 N NaOH.

AGE OF HOST

Post-emergence losses from damping-off generally diminish with in-

[1] This paper constitutes one section of a thesis submitted to the faculty of the Graduate School of the University of Pennsylvania, in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

[2] The greater part of this investigation was carried on during the tenure of a George Leib Harrison Fellowship at the University of Pennsylvania.

[3] The author wishes to express his appreciation to Dr. W. A. Campbell and Dr. B. Sleeth for valuable suggestions regarding the preparation of the manuscript.

crease in age of coniferous seedlings (10, 11). Early losses have been associated with the tenderness of the young seedlings. With the development of woodiness in the hosts, ordinary damping-off losses became relatively negligible. Early post-emergence attacks, invariably fatal, have been included in the category of ordinary or normal damping-off losses. Those occurring after this initial period, and not necessarily fatal, have been described as root-rot. Emphasis of the present studies has been placed primarily on the former type, and an attempt was made to determine how long after emergence seedlings were subject to normal damping-off attack by Fusarium species.

Initial observations on the relation between age of host and susceptibility to attack were made upon seedlings of *Pinus resinosa* grown in quartz-sand

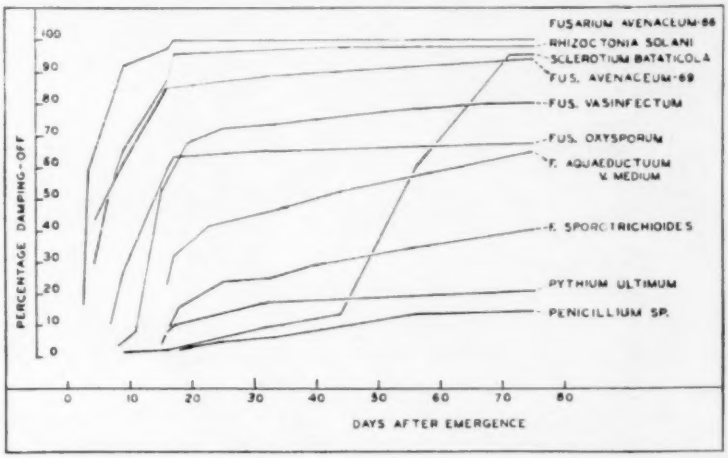

FIG. 1. Relation of time to post-emergence damping-off of *Pinus resinosa* seedlings inoculated in quartz-sand cultures with Fusarium and other standard fungus lines.

cultures, watered daily with the standard nutrient solution adjusted to pH 6. These were in 4-inch pots that had been inoculated with Fusarium or other fungus lines prior to the planting of fifty seeds in each. Periodic records were made of the losses that occurred after the emergence of the seedlings. The damping-off loss in each culture was recorded as the percentage of the total number of seedlings that had emerged up to that time.

The results are in figure 1, the curves being based upon the averages of duplicate series for each fungus line. On seedlings in contact with the more virulent fungi, effects of attack were visible soon after emergence, and maximum losses were reached within approximately three weeks. The effects of less virulent fungus lines did not become noticeable until later, although maximum losses developed before 30 days. For all of the lines there were slight increases in damping-off with time, following the initial surge of attack. Losses from *Sclerotium bataticola* were low for the first six weeks but became very pronounced thereafter, reaching an extremely high level at the termination of the experiment. This tendency for *Sclerotium* to be only

slightly effective in early attack, in comparison with *Fusarium sp.*, has already been noted (36).

In order to verify that these variations in host-pathogen relationship were due to increasing resistance of the host with age, healthy seedlings of *Pinus resinosa* of varying ages were transplanted to pots of nutrient-watered sand, that had previously been inoculated with rice cultures of *Fusarium oxysporum* and incubated at room temperature for five days. Younger seedlings were taken from a sterile germinator, whereas older ones were grown in uninfected quartz-sand in the greenhouse. Each age group was tested in duplicate, at the rate of 40 seedlings per pot, and losses due to damping-off were recorded for 30 days after transplanting. Losses in the cultures, which were run simultaneously in the greenhouse, are given in figure 2.

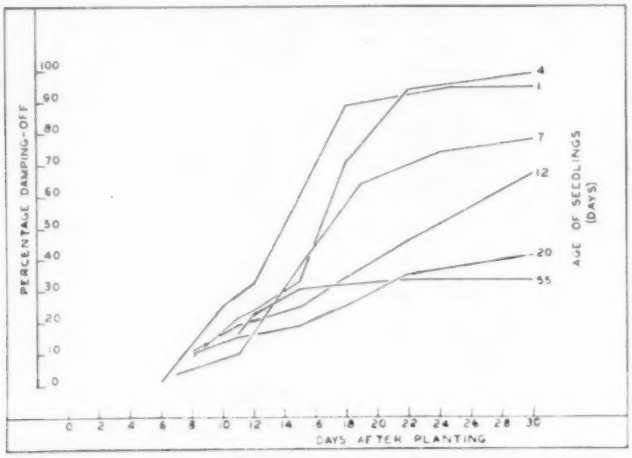

FIG. 2. Relation of age of seedlings of *Pinus resinosa* to rate and total extent of damping-off in quartz-sand cultures inoculated with *Fusarium oxysporum*.

Seedlings from 1 to 7 days old had the higher percentage of damping-off, and the reduction in levels of losses corresponded with the increasing age of the host. The time between initial exposure of the seedlings to the fungus and the first symptoms, varied from 6 days with the one-day-old seedlings to 11 days for the 55-day-old plants.

pH STUDIES

Soil reaction may affect forest-tree seedlings directly through the influence of hydrogen or hydroxyl ions, or indirectly by influencing the availability of nutrients, the physical condition of the soil, and the activity of parasitic and saprophytic soil-organisms. Conifers, in general, prefer an acid reaction for optimum seed germination (1, 4, 5, 6, 31, 37, 39) and for subsequent growth and development (6, 14, 38, 40). Species of *Fusarium*, in the laboratory, have a wide tolerance for variations in the reaction of substrates, ranging from approximately pH 2 to 11, but optimum growth has usually been observed on media of acid or nearly neutral reaction (17, 19, 20, 27).

Early observations by Gifford (9) revealed that an increase in the alkalinity of the soil by liming increased the amount of subsequent damping-off, whereas manuring treatments which tended to keep the soil reaction acid, reduced the damage. Anderson (3) observed that the application of wood ashes to seed beds before sowing increased damping-off of seedlings of *Pinus sylvestris* and *Picea sitchensis*. Hartley (10, 12) observed that damping-off in forest nurseries was not serious in soils with a pH lower than 6. In addition, soil acidification treatments have been used to control the disease (7, 10, 12, 18, 33, 35), although with only partial success in some localities.

These observations have to a large extent been confirmed by inoculation tests. Roth's investigations (29) on *Picea excelsa* inoculated in soil cultures with *Pythium deBaryanum* and *Rhizoctonia solani*, revealed no serious losses at pH values below 5.5, maximum attack on the acid side of neutrality, and again a lessening of losses at pH values above 7. The last effect is at variance with general experience in the field, where heaviest losses occur at an approximate pH value of 8 (10). Inoculations of Douglas Fir and ponderosa pine with isolates of *Pythium* and *Rhizoctonia* by Jackson (16), gave similar results. In sand cultures, however, Jackson's results showed better agreement with field experience for the higher pH values, although somewhat more damping-off at the acid levels was obtained than under natural conditions. Ten Houten (35), from inoculation tests on *Pinus nigra austriaca*, in soils that varied in pH and in organic matter, concluded that the parasitism of *Pythium deBaryanum*, *Rhizoctonia solani*, and *Fusarium oxysporum*, was highly dependent on the reaction of the soil. In those soils in which the pH was 4.5 or lower, the damage caused by these fungi was not important.

A preliminary test of the relationship of pH and soil-sterilization to damping-off was performed in soil samples artificially adjusted into a pH series according to a method used by Roth (29). A soil was prepared from three parts of loam, two of sand, and one each of leaf-mold humus and acid peat (Canada). To half of this mixture one extra part of peat was added and to the other one part of humus, yielding respective pH values of 5.1 and 6.3. By the addition of graded amounts of coarse sodium-calcium hydroxide (40 per cent NaOH, 57 per cent $Ca(OH)_2$, 2 per cent H_2O) to the more alkaline portion, samples with pH values of 6.9, 7.9, 8.3, and 8.6 were obtained. Similar treatment of the acid portion with sodium bisulphate (35–36.5 per cent H_2SO_4) yielded lots of pH 4.9 and 3.6. A mixture of the two original lots gave a sample of pH 5.6. In preliminary investigation, soil samples similarly adjusted maintained their new reactions rather closely for a long time if continually moistened with water adjusted to corresponding acidity levels. All acidity determinations, however, were made upon samples air-dried in the laboratory for several days. This method of adjusting and maintaining the acidity of soil provided samples highly comparable in physical and basic chemical content, differing mainly in respect to the acidifying and alkalizing substances added. It permitted a more significant compari-

son of the effects of the reactions on the growth of the host and the damping-off losses induced by inoculated fungi than would have been possible in a collection of soil samples from different localities.

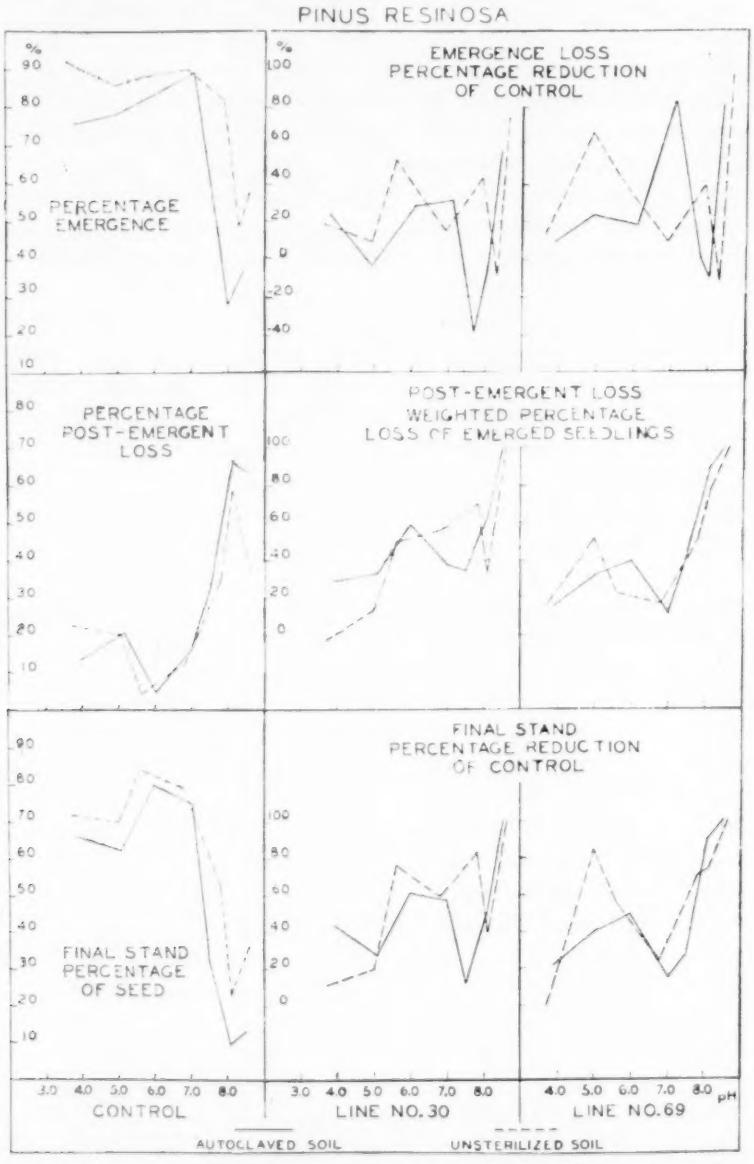

FIG. 3. Relation of pH to the growth and damping-off of *Pinus resinosa* in soil cultures inoculated with *Fusarium oxysporum* (Line 30) and *F. avenaceum* (Line 69). Results for inoculated series expressed in terms of corresponding control data.

Each pH lot was distributed into twelve 7-inch pots, and six of each group were autoclaved at 15 pounds for one hour on two successive days. The resultant pH values in the autoclaved samples were 3.8, 4.9, 6.1, 7.1, 7.7,

8.0, and 8.4. Duplicate pots were then inoculated with rice-mush cultures of *Fusarium oxysporum* (Line 30) and *F. avenaceum* (Line 69), sterile rice medium being added to the control series. After incubation for one week

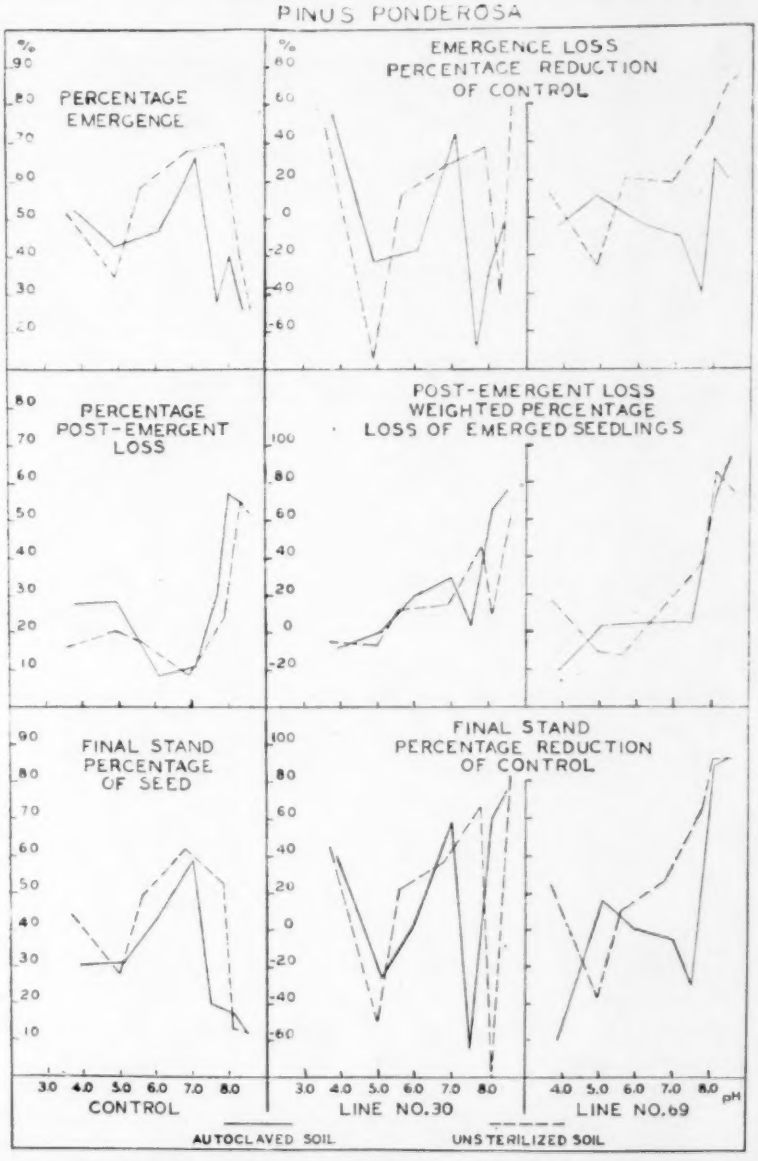

FIG. 4. Relation of pH to the growth and damping-off of *Pinus ponderosa* in soil cultures inoculated with *Fusarium oxysporum* (Line 30) and *F. avenaceum* (Line 69). Results for inoculated series expressed in terms of corresponding control data.

at room temperature, 50 seeds each of *Pinus resinosa, Pinus ponderosa,* and *Pinus sylvestris* were planted in each pot, and all series were placed in the greenhouse.

Emergence and post-emergence losses were tabulated during 5 months. At the termination of the experiment a survival count was made and the final pH of the various soils was measured. To evaluate the effects of the inocu-

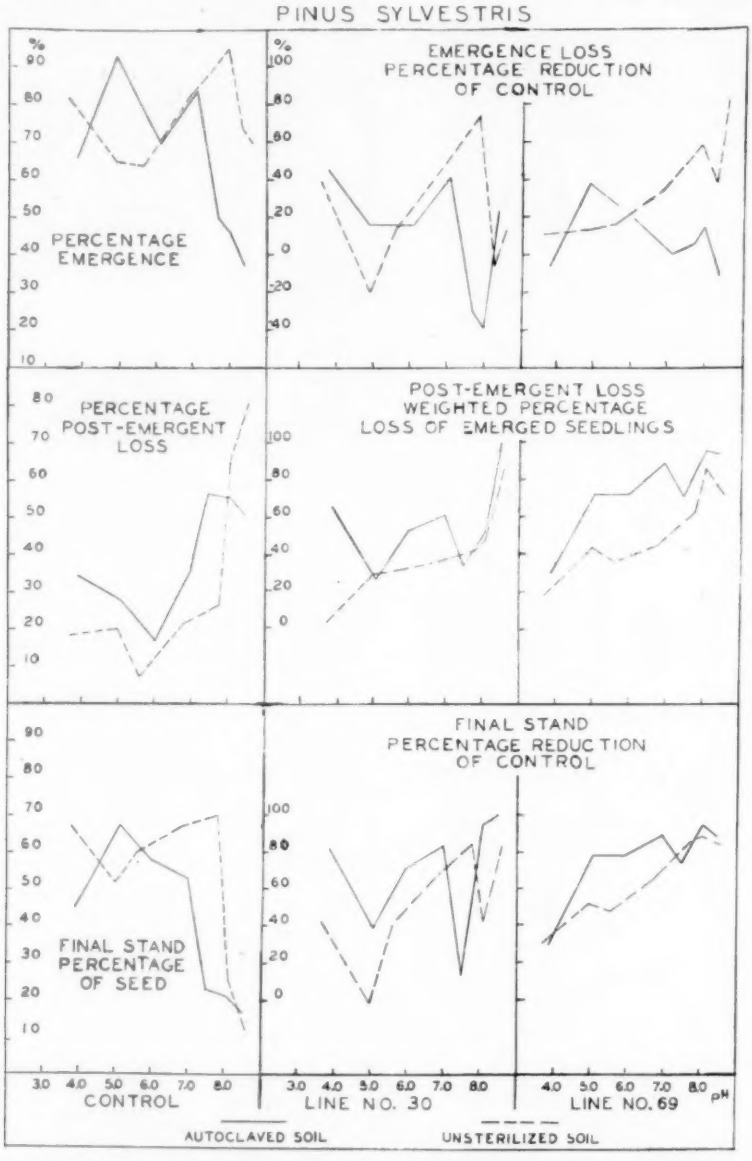

FIG. 5. Relation of pH to the growth and damping-off of *Pinus sylvestris* in soil cultures inoculated with *Fusarium oxysporum* (Line 30) and *F. avenaceum* (Line 69). Results for inoculated series are expressed in terms of corresponding control data.

lations alone at the various pH levels, apart from those losses occurring as a result of the growth of the hosts in some instances in a physiologically unsuitable environment, seedling losses in inoculated pots were calculated in

terms of corresponding control data. The weighted results are given in figures 3, 4, and 5, which also include the original control results for purposes of comparison. Emergence data are plotted against initial pH values, and those for post-emergence loss and final stand against the average reactions that prevailed during the experiment.

The differences in pH, or their indirect effect, exerted a pronounced influence upon the relative emergence of the hosts, and also affected their ability to survive. Attempts to isolate organisms from seedlings that died in control pots showed that fungi could not be isolated from approximately half the seedlings, and that from infected seedlings, Fusarium isolations were no more numerous than other contaminants.

TABLE 1.—*Final concentrations in parts per million of some constituents determined by dilute-acid extracts of soil samples adjusted and maintained in a pH range. A blank test indicates the substance is low beyond the sensitivity of the test reaction. The values for pH are average for the duration of the experiment*

Ions	pH values for autoclaved soils						
	3.9	5.1	6.0	7.0	7.5	8.1	8.5
Ca	40	110	115	160	150	165	175
K	0	0	0	0	0	0	0
NO_3	1–2	10	8	5	5–8	18	20
NO_2	0	0	0	tr	1	tr	tr
NH_3	5	6	2–3	0	tr	2	1
Mg	1–2	5	7–10	8	10	15–20	8
P	2	4	5–6	10	45	25	30
SO_4	30	120	10	0	0	0	0
	pH values for unsterilized soils						
	3.7	5.0	5.6	6.8	7.8	8.1	8.6
Ca	40	100	90	165	175	250	200
K	0	0	0	0	0	0	0
NO_3	5–10	15	5	2	4–5	10–14	60
NO_2	0	0	0	0	1	1	tr
NH_3	3	2	tr	0	1–2	1	1
Mg	1–2	3	8–10	12–16	10–12	12–14	12
P	2–3	5	5	8–10	15–16	45	55
SO_4	50	100	0	tr	0	0	0

At the several levels of acidity, there were pronounced differences in host-response with respect to emergence, survival, and damping-off to two Fusarium lines, both in autoclaved and unsterilized soils. However, there was no indication whether the effects were due to reaction differences directly, or to the indirect results of the chemical changes induced by the treatments of the soil samples. Analyses made at the termination of the experiments upon the uninoculated soil samples, according to the methods of Spurway (34), showed significant differences in the availability of certain constituents at the different levels of reaction, and between autoclaved and unheated samples. The results of these analyses are given in table 1. Certain of these differences could have been anticipated from the manner of soil treatment. Thus the increase in Ca availability with the rise in alkalinity

and of the SO_4 ion in the acid samples are understandable. The latter, however, gave a higher test at pH 5 than at the more acid levels to which it had been added in greater amounts. In view of similar variability of the other

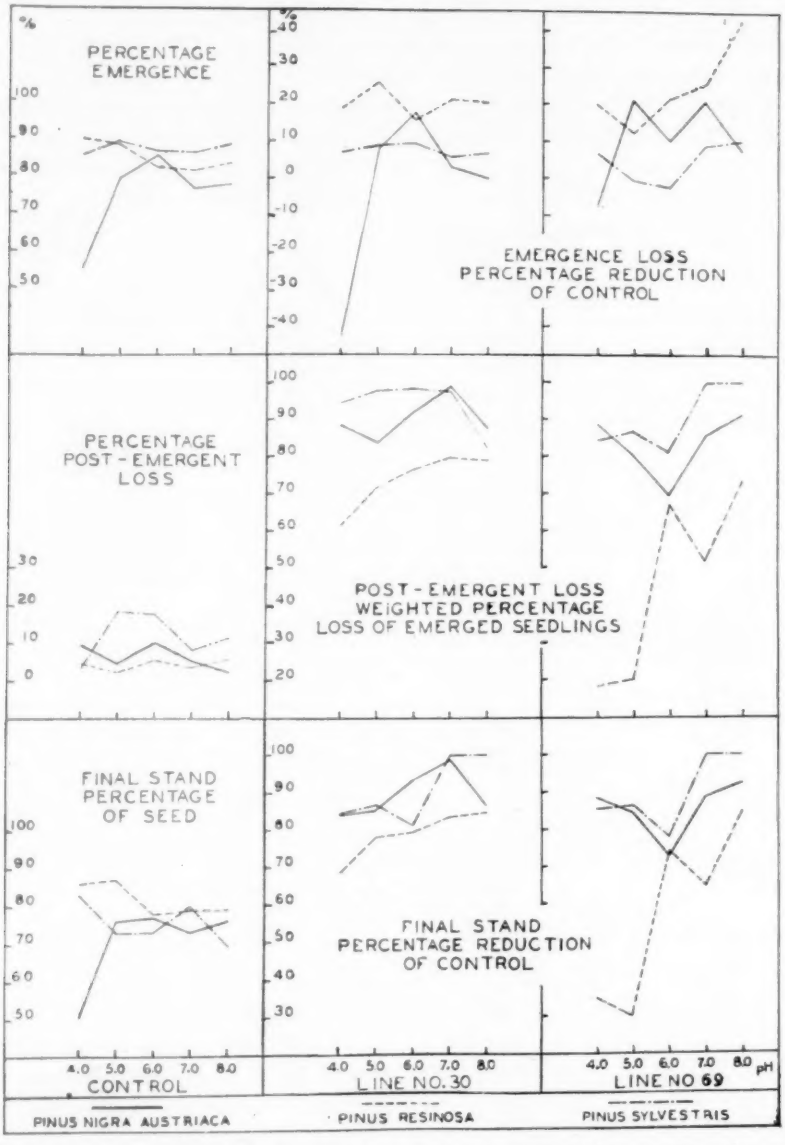

FIG. 6. Relation of pH to the growth and damping-off of three conifers in quartz-sand cultures inoculated with *Fusarium oxysporum* (Line 30) and *F. avenaceum* (Line 69). Results for inoculated series are expressed in terms of corresponding control data.

constituents, further experiments were necessary, in which the factors of reaction and nutrition could be independently controlled.

In order to establish the relationship of acidity alone to the development

and damping-off of conifers, inoculation tests were made in quartz-sand (Ottowa) substrates, watered by flooding daily with the basic nutrient solution adjusted in pH at one-unit intervals from 4 to 8 inclusive. The experiments were in duplicate on three hosts inoculated with two fungi, *Fusarium oxysporum* (Line 30) and *F. avenaceum* (Line 69). Fifty seeds of *Pinus resinosa* and 50 of *Pinus sylvestris* were sown separately in four-inch pots, and the same number of seeds of *Pinus nigra austriaca* in five-inch pots, all of which had been inoculated five days previously with rice cultures of the fungi. Control series received sterile rice mush. Emergence and losses were recorded for two months. The results, recalculated according to the method described, are summarized in figure 6.

Corresponding studies were made upon the effects of acidity variations

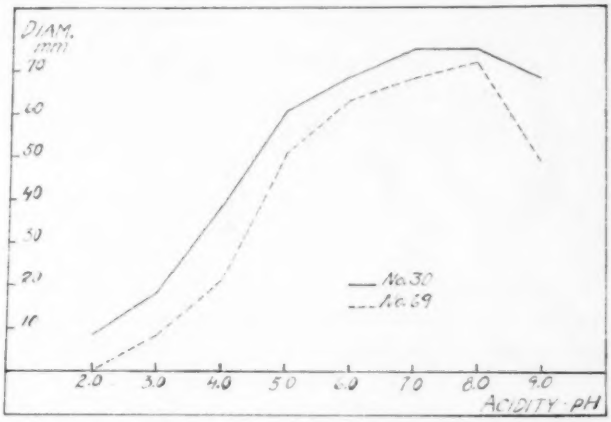

FIG. 7. Effect of acidity on the growth of *Fusarium oxysporum* (No. 30) and *F. avenaceum* (No. 69) on potato-dextrose agar.

upon the growth of the two Fusaria in Petri plates on potato-dextrose agar. The pH varied by one unit from 2.0 to 9.0, each treatment replicated five times. After incubation for six days at 28° C., two diameters at right angles were measured for each culture and averaged (Fig. 7).

NUTRITION

The concentration of the nutrient solution is an important factor in the growth and tolerance to environmental conditions of coniferous seedlings (8, 24, 25, 26, 41). A deficiency in any of the essential nutrients or an unbalanced ratio, as may well be induced by prevalent acidity conditions (13, 22, 28), influences the entire metabolic process, and as a consequence, may decrease the resistance of the seedlings to physiological and infectious diseases. Similarly, Fusarium species, as well as other soil organisms that may be potential damping-off agents, have specific nutritional requirements (17, 21, 27, 42), and the effects of alterations in concentration of nutrients, with changes in acidity, may conceivably be the underlying or a contributing factor to the various levels of pathogenicity of these organisms.

Nutritional aspects of the growth and damping-off of *Pinus resinosa* were studied in sand cultures, with excesses and deficiencies of calcium, phosphorus, nitrogen, magnesium, potassium, and sulphur in the standard nutrient solution. Since the original nutrient solution contained certain salts supplying two of these elements, in order to eliminate either one of them it was necessary to replace an equivalent concentration of the remaining constituent of the compound by sodium-salt or metallic chloride, depending upon whether it appeared as an anion or cation. An excess of any element was attained by trebling its molar concentration by the addition to the basic

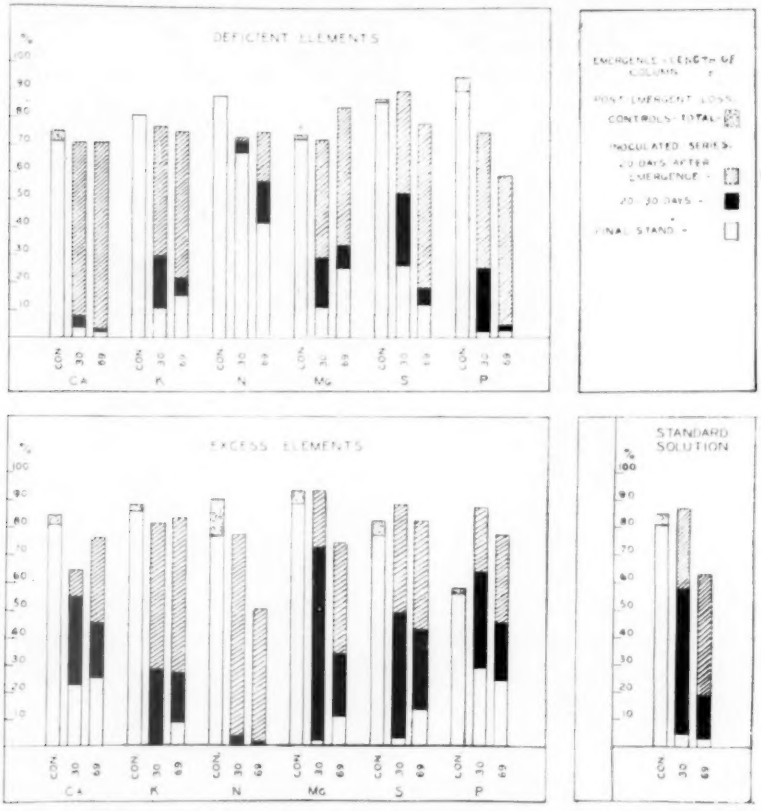

FIG. 8. Effects of deficiencies and excesses of various elements on emergence and damping-off of *Pinus resinosa* inoculated in quartz-sand cultures with *Fusarium oxysporum* (Line 30) and *F. avenaceum* (Line 69). Results are averages of duplicate trials.

solution of twice the original concentration of the particular ion as chloride or sodium-salt. In the case of phosphorus, additional treatment was necessary. Since originally this element was supplied in a glycerophosphate salt, used also as a source of carbon for the fungi, the removal of this ion from the solution necessitated the addition of an equivalent concentration of some carbon source, in this case dextrose. Conversely, an excess of phosphorus was attained by the use of Na_2HPO_4, in order not to increase the basic carbon content of the solutions. All solutions before use were adjusted to a final pH of 6.

TABLE 2.—*Results of the growth of Pinus resinosa seedlings in quartz-sand cultures deficient in certain elements. Duration of experiment 30 days following emergence. Daily mean temperature range 68–75° F.*

Element	No. of seedlings	Average length in millimeters		Average weight in milligrams		Ratio of green to dry weight
		Roots	Hypocotyls	Green	Dry	
Ca	23	13.7	43.9	43.4	4.6	9.4
K	21	11.2	39.3	33.9	5.5	6.2
N	30	21.5	42.4	45.6	7.1	6.4
Mg	11	10.9	35.3	43.5	5.3	8.2
S	30	12.6	39.9	44.0	4.7	9.4
P	27	12.7	43.3	44.6	3.9	11.4
Full	30	13.4	43.7	44.0	6.0	7.3

The inoculation procedure was modified to prevent any great change in the concentrations of the various nutrients which might result from the addition of rice to the substrate. *Fusarium oxysporum* and *F. avenaceum* were grown on 50 cc. of an aqueous extract of boiled rice, to which had been added 0.5 per cent dextrose. After incubation for three weeks at 28° C., the mycelial mats were removed, thoroughly washed with distilled water, and then ground with sterile sand in a mortar. This was distributed as inoculum, at the approximate rate of one-half mat per pot, into four-inch pots of autoclaved sand, which were subsequently saturated with the various nutrient solutions. The pot cultures were incubated for five days at room temperature and 50 seeds of *Pinus resinosa* were then sown in each. Duplicate series for both fungi and controls were maintained for 30 days following general emergence of the seedlings, the pots being watered daily by flooding with the corresponding solutions.

The results are given in figure 8. At the termination of the experiment, the seedlings were removed from the substrate and certain growth characteristics measured. These have been summarized in tables 2 and 3.

The responses of *Fusarium oxysporum* to nutritional conditions were tested in 5 replicates on agar substrates (1.5 per cent) in Petri dishes, pre-

TABLE 3.—*Results of the growth of Pinus resinosa seedlings in quartz-sand cultures with excesses of certain elements. Duration of experiment 30 days following emergence. Daily mean temperature range 68–75° F.*

Element	No. of seedlings	Average length in millimeters		Average weight in milligrams		Ratio of green to dry weight
		Roots	Hypocotyls	Green	Dry	
Ca	30	20.5	38.4	41.2	5.7	7.2
K	30	19.5	39.6	43.0	5.7	7.5
N	22	18.6	38.8	42.8	5.9	7.3
Mg	36	20.6	38.9	44.7	5.5	8.1
S	35	19.2	39.1	41.8	5.6	7.5
P	24	18.2	37.7	43.5	5.8	7.5
Full	32	20.1	39.9	46.0	5.6	8.2

pared from solutions containing corresponding excesses and deficiencies of elements, and adjusted to yield pH 6 after sterilization. The average diameter of each colony was determined after incubation for 6 days at 28° C. The results, given in table 4, indicate significant differences in the growth of the fungus under the several conditions. Removal of a single element in each case reduced the growth in comparison to that on the standard solution.

TABLE 4.—*Results of the growth of Fusarium oxysporum in synthetic-nutrient agar containing deficiencies and excesses of certain elements*

Element	Average diameters of colonies in mm.	
	Deficiency	Excess
Ca	74.7	84.5
K	69.0	81.4
N	65.7	86.4
Mg	72.6	80.1
S	69.4	82.6
P	67.6	78.5
Full	82.4	

DISCUSSION

Inoculations in sand cultures, adjusted over a pH range, with two species of *Fusarium* upon three coniferous hosts, revealed, on the average, a direct correlation between reaction and damping-off. Although variance was evident in the reactions of the hosts among themselves and between fungus treatments, a definite trend nevertheless was indicated for losses to become greater with decreasing acidity. The differences in parasitism at the various pH levels were most likely dependent upon the direct effect of the reaction of the media on the growth of the pathogens. With the single exception of the reduction in emergence of *Pinus nigra austriaca* on the most acid medium, different levels of reaction apparently had no significant effects upon the hosts, measured in terms of emergence and survival. In contrast, however, both fungi were directly affected by the changes in acidity, and their relative growth at the various levels was directly correlated with the losses induced. Jackson (16) also has interpreted the lower losses under more acid conditions with inoculations of *Pythium* and *Rhizoctonia* on conifers in sand and liquid cultures, in terms of a direct effect of the reaction on the growth of the parasites.

The results of soil tests of reaction differences indicated a far greater variability for damping-off as well as for emergence and survival of hosts in uninoculated controls. In both autoclaved and unsterilized soils, losses were generally negligible or moderate at the extreme acid end of the range. Maxima were reached approaching neutrality and the losses dropped sharply in most cases at pH 7.5 and 8.0, to be followed later by severe or complete losses at the most alkaline values. Roth (29), reporting results from a study of the effect of pH on the damping-off of Norway spruce (*Picea excelsa* Link) grown under somewhat similar soil conditions, found losses caused by *Cor-*

ticium vagum and *Pythium deBaryanum* definitely increased from pH 3.8 to maxima between 6.5 and 7.0 and then decreased at pH 8.0. These facts agree to some extent with the present results, although they were not extended so far with regard to more alkaline substrates.

The variance between the results derived from sand- and soil-cultures undoubtedly resulted from the additional chemical variability in the latter. Deficiencies and excesses of certain elements which varied in the soil cultures, tested under controlled conditions of reaction in sand-culture, were associated with losses from damping-off. It was frequently possible to correlate the magnitude of the attack with the simultaneous effects of these nutritional conditions upon the host and pathogen. Varying nitrogen gave the most pronounced differences in this respect. Where this element was deficient the growth of the fungus was least, whereas the host had optimum root development as well as a relatively low degree of succulence, expressed as ratio of green to dry weight. There was little loss from damping-off. An excess of nitrogen, although mildly affecting the host by a slight reduction of root length, unquestionably stimulated fungus growth sufficiently to account for the rapidity and severity of its subsequent attack. Hartley (10) has likewise expressed the belief, based on general nursery experience, that conifers grown on a soil rich in nitrogen are especially susceptible to damping-off.

Illick and Augenbaugh (15), in studies on *Pinus rigida,* stated that an excess of lime in the soil creates conditions which are most favorable for the activities of damping-off fungi, although no mention is made of any direct effect of excess lime on the seedlings. In the present experiments, a deficiency of calcium, inducing a high degree of succulence of the seedling, combined with the best fungus growth of the entire deficiency series, resulted in early and heavy attack. On the other hand, an excess of calcium yielded a hardened seedling with good root development, by virtue of which the host apparently was able to withstand rather good growth of the fungus. This suggests that the high mortality associated with alkaline calcareous soils is due to the reaction directly rather than to the high calcium content. In fact, Albrecht and Jenny (2), in studies of the damping-off of soy bean seedlings, concluded that within a wide range of pH (3.8–8.0), heavy damping-off occurred only when the calcium supply was low, but none took place when the supply of calcium was high. Chapman (6) indicated that pH and soluble-calcium content may independently influence survival of shortleaf pine (*Pinus echinata* Mill.); the latter factor, however, restricting survival with concentrations of 500 parts per million or higher. Howell (14) observed that calcium is not deleterious to seedlings of *Pinus ponderosa,* and suggested that the fact that the ion is not assimilated by the plant in alkaline soils may be important. In the soil experiment of the present investigations, the calcium content was increased simultaneously with the alkalinity of the medium, and the higher losses that resulted may have been due to the masking of the beneficial effect of calcium, present in less than toxic concentrations, by the alkaline environment.

The concentration of phosphorus likewise markedly affected the growth of the host as well as the extent to which it damped-off. Under a deficiency of this element, the seedlings were the most succulent of the entire lot and were extremely susceptible to attack in spite of the fact that the fungus grew rather poorly. With an excess of phosphorus, the seedlings became moderately hard and the fungus growth was poorest of the entire excess series, both factors combining to yield a relatively lower level of attack. Availability of this element appeared to be a factor related to the reduction of losses in the soil experiments on the alkaline side of neutrality. These low points generally occurred at pH 7.5 in the autoclaved soils and at 8.1 in the unsterilized lots. Both points coincided with a high content of available phosphorus. The availability of this element has been associated with buffering of plant cytoplasm and cell sap (6), its reduction in the substrate being associated with a lower degree of buffer capacity for alkali. Addition of superphosphate to an acid nursery soil in which seedlings were developing, somewhat increased the ability of the plants to withstand a wide range of environmental conditions (14).

Damping-off of the seedlings, under the influence of variations in the concentrations of the other elements tested, was less consistent than were the effects of the conditions upon the hosts. In general the reduction of losses where the test elements were deficient, as compared with the control, appeared to be related to the corresponding reduction in growth of the fungi. In those media in which all the elements were present in their basal concentrations, the growth of the colonies appeared little influenced by specific excesses, and the losses were comparable with those in the standard solution. Young and Bennett (42) have shown that the proper balance of the inorganic constituents in the solution is essential for the maximum growth of *Fusarium oxysporum* and other fungi. In the present experiments, this balance was more affected by the removal of an element from the nutrient solution than by an increase in its concentration.

The chemical factors were connected with steam sterilization of soil. Heating the soil produces pronounced chemical and biological changes (10, 23, 30, 32), which must be considered in evaluating the treatment to control damping-off. Lindfors (19) concluded that steam-sterilization of soil created conditions favorable for reinfection by Fusarium. Ten Houten (35) found a similar increase in attack with *Rhizoctonia solani* on sterilized soil, and attributed the higher damage to the removal by the heating process of organisms antagonistic to the pathogen. A similar view was taken by Hartley (10). Scheffer (30) observed that a heat treatment of soil was not detrimental to subsequent growth of several conifers; in fact, plants grown in the heated soil developed somewhat better roots and crowns. However, as indicated by the results of the present experiments as well as other observations (23, 32), steam sterilization may change the reaction of a soil as well as its basic nutritional equilibrium. Some of these factors may operate independently, or in combination, upon host and pathogen alike to affect directly the

amount of disease. Thus the effectiveness of the treatment depends upon whether the conditions favor or oppose the relationship. The present results have indicated that the treatment increased subsequent losses as often as it reduced them, with no apparent consistency, over the entire range of soil samples. Similar conditions in the field undoubtedly account for the variability and contradiction of the reports on the usefulness of this method.

SUMMARY

In seedlings of *Pinus resinosa* grown in quartz-sand culture and inoculated with Fusaria and other fungus lines, losses due to more virulent fungi appeared relatively early and reached their maximum levels within approximately three weeks following emergence, whereas those due to less virulent lines were delayed, although generally reaching maximum levels before thirty days. Losses from *Sclerotium bataticola*, a comparison line, were low for the first six weeks, but increased thereafter and attained a high level before seventy-five days.

Tests with seedlings of various ages, inoculated with *Fusarium oxysporum* under identical conditions, demonstrated that resistance to invasion increased directly with increasing age of *Pinus resinosa*.

The relation of acidity to damping-off was tested in cultures of a single soil the pH of which was varied artificially. In samples, subdivided to include autoclaved and unsterilized lots, emergence reductions of three coniferous species due to inoculations with *Fusarium oxysporum* and *F. avenaceum* were generally low or moderate at pH values in the acid range and high above pH 8. In some cases emergence in inoculated pots was greater than in corresponding controls at pH 7.5 in autoclaved samples and at pH 4.9 and 8.3 in unsterilized soils. Post-emergence damping-off was low in more acid samples, reached a maximum on the acid side of neutrality, fell off sharply in the autoclaved soil at pH 7.5 and in the unsterilized soil at pH 8.1, and then became uniformly high in the most alkaline substrates. Differences were not consistent at the various levels of acidity from autoclaved and unsterilized soil samples. The chemical variability in the soil samples, which resulted from the induction of reaction differences and from steam-sterilization is discussed.

In quartz-sand cultures of varying pH, losses of three conifers inoculated with the same fungi were generally high at all levels of acidity, although there was some tendency for increased damping-off with increasing alkalinity.

Tests in quartz-sand cultures on the effects of variations in the concentration of certain constituents of the nutrient solution, under uniform conditions of reaction, demonstrated that the influence of nutritional factors on damping-off could be correlated with their simultaneous effects upon the host and pathogen. The magnitude of the loss was associated with the growth of the pathogen and the degree of susceptibility of the host, measured in terms of its succulence. A deficiency of nitrogen gave relatively negligible

losses, whereas an excess caused early and heavy attack. Deficiencies of calcium and phosphorus resulted in high damping-off losses, which were considerably reduced when these elements were present as excesses. When potassium, sulphur, and magnesium were deficient, final stands were somewhat higher than under excesses of these elements, the latter resembling controls grown and inoculated in standard solutions.

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THE EFFECT OF ARTIFICIAL LIGHT ON GERMINATION OF UREDIOSPORES OF PHRAGMIDIUM MUCRONATUM (FR.) SCHLECHT.[1]

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INTRODUCTION

Dillon Weston (2, 3, 4) found that the germination of urediospores of *Puccinia graminis tritici* is inhibited by intense light of the visible range. Separation of white light into its components demonstrated that the inhibitory effect is a property of the longer rays (red, orange, yellow) of the spectrum; germination was not affected by blue or green light.

Stock (10) reports no effect of strong artificial light on the germination of urediospores of *Puccinia triticina, P. dispersa,* and *P. coronata,* except a slight delay in the last two species in the time of movement of the spore protoplast into the germ tube. In the case of *P. graminis* the germination was somewhat delayed by strong light, but the eventual germination was as high in the light as in the dark.

A similar retarding influence of diffuse sunlight has been found in the case of *Puccinia glumarum tritici* (11).

Negative phototropism of germ-tube growth has been observed in the case of species of *Puccinia* (6, 7).

Studies on other rusts (5, 8) have failed to establish any effect of light on urediospore germination.

The data here presented were obtained during a general investigation of the physiology of spore germination in *Phragmidium mucronatum* (Fr.) Schlecht., cause of the common leaf rust of cultivated roses.

MATERIALS AND METHODS

A single-urediospore line of the pathogen was propagated on the variety Briarcliff and used in all experiments. This clone was isolated originally from infections on leaves of the variety Christopher Stone received from California.[2]

Mature urediospores were brushed from the sori into a beaker, then transferred to a small "puff-duster" made of glass tubing. The spores were blown from this onto the surface of 2 per cent water agar contained in 7-cm. Petri dishes. Methods of collection and germination are more fully described elsewhere (1).

The experiments were made in a thermostatically controlled constant-temperature room. The light source was a 500-watt "Mazda" CX bulb.

[1] Excerpt from a thesis presented April, 1944, to the faculty of the Graduate School of Cornell University, in partial fulfillment of the requirements for the degree of doctor of philosophy.

[2] The writer is indebted for the original rust material to Dr. H. Earl Thomas, Dept. of Plant Pathology, University of California, Berkeley, Cal.

Interposed between the light and the germination surface were a layer of water, a thin sheet of window glass, and a Corning "AKLO" No. 395 filter. This filter was selected so that, in combination with the filtering action of the water layer, practically all of the infra-red rays were screened out. Various light intensities were obtained by placing the germination dishes at appropriate distances from the light source. Light intensity was measured with a Weston Model 603 light meter equipped with a "Viscor" filter.

The significance of observed differences in germination was determined by means of the Chi-square test (9).

RESULTS

A preliminary experiment demonstrated a marked inhibition of germination at a light intensity of 3,000 foot-candles and a temperature of 22–24° C. Germination was 79.2 per cent in controls held in the dark at this temperature, 17.1 per cent in lots exposed to the light.

TABLE 1.—*The influence of various intensities of artificial light on urediospore germination. Checks B, D, and F wrapped in black paper and lead foil; checks G, H, and I in dark chambers*

Series	Light intensity, foot-candles	Temperature, °C.	Per cent germination[a] at		
			3 hr.	6 hr.	24 hr.
A	1250	19.5–20.0	7.0**	28.6**	42.2**
B	0 (check)	19.5–21.5	85.0	92.9	93.7
C	200	19.0–20.0	80.4**	91.8	93.0
D	0 (check)	19.0–20.0	87.0	91.2	92.3
E	2.4	19.0	88.2	92.2	90.8
F	0 (check)	19.0	87.8	91.6	92.1
G	0 (check)	18.0	87.4	92.2	93.9
H	0 (check)	21.0	86.4	92.6	92.8
I	0 (check)	25.0	27.0	62.6	62.4

[a] Three- and six-hour counts based on 2 replicate samples of 250 spores each; 24-hour count based on 4 samples of 250 spores each.

Double asterisk indicates that germination differs significantly (99.1) from that of corresponding check.

A comprehensive experiment to measure the effect of various light intensities on the rate of germination and its final value is summarized in table 1. Since the optimum temperature for urediospore germination in *Phragmidium mucronatum* is 15–21° C. (1), the highest light intensity tested was one that did not raise the temperature above 21° C.

Three sets of 4 Petri dishes were sown and placed in the lighted chamber so as to receive light of three different intensities—1,250, 200, and 2.4 foot-candles. Similar plates wrapped in black paper and lead foil were placed adjacent to the exposed plates to serve as checks. Temperature was recorded periodically from wrapped and unwrapped thermometers at the 3 stations. Wrapped thermometers were enclosed in black paper and laid horizontally beside the germination plates. Lead foil was not used in wrapping these thermometers since it seemed that the heat-trapping effect of the black paper

wrapping would ensure that the maximum temperature would be reached. The temperature of the unwrapped plates was arrived at by periodic readings of unwrapped thermometers resting horizontally on the table beside the plates.

A further series of checks (Table 1, G, H, and I) consisted of replicate plates sown with spores and held in the dark in temperature chambers at 18°, 21°, and 25° C. respectively.

The injurious effect of light at 1,250 foot-candles intensity is clearly demonstrated (A). Both the rate of germination and the final value reached are significantly lower than the control (B). Chi-square comparisons show that only in the plates exposed to light of 1,250 foot-candles intensity was the attainment of the final level of germination delayed beyond 6 hours; in all other plates the germination at 6 hours was as high as that at 24 hours.

Light at an intensity of 200 foot-candles (C) exerted a slight delaying action on spore germination. This effect was evident at 3 hours from sowing, not at 6 or at 24 hours, *i.e.*, there was no permanent inhibition.

At the lowest intensity tested, 2.4 foot-candles, light had no effect on germination (E). The plates of this treatment were placed laterally in relation to the light source, but no evidence of phototropism of germ-tube growth could be seen. Other plates (A, C) that were illuminated were directly under the light source and therefore offer no data on phototropism.

None of these effects can be explained on the basis of temperature, with the necessary reservation that temperatures inside of the spore cannot be measured and may exceed air temperature. In all cases the temperatures of the wrapped check plates (B, D, F, in table 1) were as high as those of the lighted plates. Furthermore, germination in the dark at 25° C. (I) was significantly higher at all times than germination on plates at 19.5–20.5° C. and high light intensity (A).

Effects of ultraviolet rays may be excluded, inasmuch as the light passed through a layer of window glass and the glass Petri-dish lid before reaching the spores.

Spores that had been exposed for 24 hours to light of high intensity (Table 1, A) were removed to a dark chamber at 18° C. After 24 hours under these conditions, germination had increased from 42.2 to 54.5 per cent. In other words, 21 per cent of the spores that had failed to germinate during the exposure to light were still viable at the end of that period, 79 per cent were dead.

Dry spores in thin-walled glass vials were exposed to light of 1,250 foot-candles intensity for 24 hours at 21° C. Germination of these spores at the end of this period was not significantly different from that of control spores held in the dark.

DISCUSSION AND SUMMARY

Under strong artificial light (1,250 foot-candles) both final germination and rate of germination of urediospores of *Phragmidium mucronatum* on

water agar were depressed. For the great majority of the illuminated spores this phenomenon was not merely inhibition but was a lethal effect. A test of germination in the dark of previously illuminated spores showed that only 21 per cent of the ungerminated spores were germinable after 24 hours exposure, the larger proportion of the spores having been killed by the exposure to light.

It is, however, possible that the apparent lethal effect of strong light is only indirect. Spores prevented from germination, but not otherwise injured, by the light may have lost their viability as the result of the leaching of soluble cell constituents into the agar medium. Unpublished experimental investigations demonstrated that spores on agar lose their viability rapidly if prevented from germinating by low temperatures. In one such case storage of spores for 24 hours on agar at 3° C. resulted in a decline in viability from 91.1 to 25.4 per cent.

The subsequent germinability of dry spores was not affected by an exposure of 24 hours duration to light of an intensity of 1,250 foot-candles.

For the sake of comparison with natural conditions it may be noted that light intensity at midday in the summer commonly reaches the value of 10,000 to 12,000 foot-candles.

Spores germinating on agar under an illumination of 200 foot-candles intensity were slightly delayed in germination relative to unlighted controls at the same temperature. The inhibitory effect of light of this intensity was evident only during the first 3 hours of the germination period.

Light of low intensity (2.4 foot-candles) had no effect on urediospore germination. There was no evidence of phototropism of germ tube growth when the germinating spores were illumined laterally by light of this intensity.

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LATE BLIGHT FORECASTING SERVICE[1]

WAR SERVICE COMMITTEE OF THE UPPER MISSISSIPPI VALLEY PLANT PATHOLOGISTS
I. E. MELHUS, CHAIRMAN, SUB-COMMITTEE ON LATE BLIGHT

In 1943 late blight forecasting was undertaken as a war service by a sub-committee of the "War Service Committee of the Upper Mississippi Valley" Plant Pathologists.[2] The estimated loss of 25,000,000 bushels of potatoes in 1942 called for prompt and coordinate action of each and every State and Province in the region. The project received its initial impetus following the reading of a paper entitled "The Late Blight Outbreak of 1942 and a Proposed Forecasting Service" before the Iowa Vegetable Growers Association meeting in the fall of 1942. As a result of the proposal outlined for Iowa, R. J. Haskell called together representatives of different state potato certification agencies present to consider preparations for combatting late blight on a regional basis in 1943. Those present were M. B. Moore and A. G. Tolaas of Minnesota, R. D. Butcher of North Dakota, H. M. Darling of Wisconsin, E. P. Barrios of South Dakota, John McLean of Colorado, G. C. Kent, E. L. Waldee, and I. E. Melhus of Iowa.

The problem of being prepared to combat late blight was considered from the standpoint of forecasting, spraying, and availability of spray materials. Everyone present was keenly interested in blight control and believed much would be gained through a forecasting service. The several inspection agencies present were prepared to render all possible service.

Those present unanimously endorsed the following statement: "Because of the likelihood of destructive epiphytotic development of late blight of potatoes in 1943, due to the abundant and widespread distribution of inoculum in potato seed stocks, it is urged that Extension Pathologists and others cooperate to the fullest extent in providing for a blight development intelligence service and in preparing growers for quick and effective spraying to prevent a repetition of the great losses of 1942."

The sub-committee was organized with representatives from each State and the two Prairie Provinces of Canada in the region to report the weather and the state of development of the late blight pathogen in their respective States or Provinces. These data were sent to the chairman at Ames, Iowa, as they became available. He, with the assistance of Mr. Hans Frey in 1943 and Dr. Edgar F. Vestal in 1944, tabulated the data and issued the reports and forecasts.

TEMPERATURE, RAINFALL, AND LATE BLIGHT PREVALANCE AND DESTRUCTIVENESS

In figure 1 are recorded the temperature and rainfall from 1941 to 1944 inclusive for Illinois, Indiana, Iowa, Michigan, Nebraska, North Dakota,

[1] Journal paper No. J–1296 of the Iowa Agricultural Experiment Station, Ames, Iowa, Poject No. 450.

[2] W. E. Brentzel, W. F. Buchholtz, J. H. Craigie, Carl J. Eide, W. J. Henderson, James H. Jensen, G. C. Kent, William A. Kreutzer, R. H. Larson, L. R. Tehon, M. B. Linn, J. E. Livingston, J. H. Muncie, R. C. Rose, R. W. Samson, Paul Tilford, T. C. Vanterpool, I. E. Melhus, Chairman.

South Dakota, Minnesota, and Wisconsin. Temperature and rainfall data for Manitoba are not at hand, through no fault of the pathologists of that Province, but a report for the Province will be included. The amount of late blight was so small in Missouri and Kansas and the Province of Saskatchewan that no attempt was made to correlate the temperature and rainfall with the late blight occurrence.

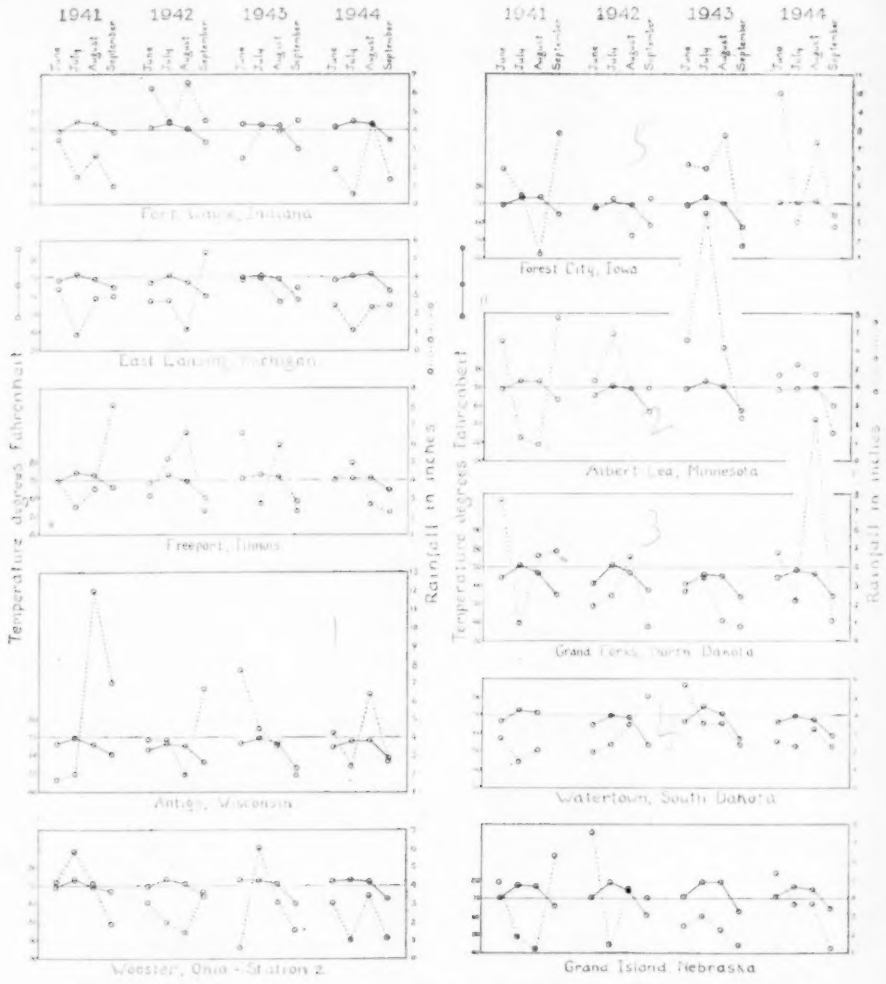

FIG. 1. Monthly mean temperature and rainfall in nine States, 1941–1944.

At the outset it should be pointed out that the available data from the respective States were limited; the weather records from only one station were used. Sometimes the chosen station was not in the potato growing region. In other cases the disease survey was very limited because no one was available to make the observations and there was often little uniformity in the records. On the other hand, in attempting to learn whether a fore-

casting service could be established in a large region, the lack of extensive data may well have been an advantage in testing the feasibility of the undertaking.

In any event, imperfect as the records were, and granting that some mistakes may have been made, it is significant to know that by using the influence of temperature and rainfall on the development of the organism, its destructiveness can be predicted.

The line at 70° F. in figure 1 designates the temperature above which growing conditions were not highly favorable for the late blight organism in its initial stages of development. In no case has late blight become seriously destructive where the mean temperature was above 70° in June and July. The 70° point was of much assistance in formulating a basis for predictions as the reports arrived from the committee members.

For an outbreak of late blight to develop, three conditions must be fulfilled: first, there must be a source of inoculum, such as infected seed pieces, cull piles, volunteer potatoes, etc., second, the temperature and moisture conditions must be such that the pathogen can grow and fruit, and, third, there must be abundant susceptible host tissue readily available. The first and third conditions prevail almost every season, but the second is more rare. The organism survives in seed in storage, is carried to the field and planted, or it may survive in cull piles or dump piles near villages and farms where potato houses are located.

The Upper Mississippi Valley States rather readily fall into at least three groups with respect to temperature. The eastern section consisting of Ohio, Indiana, and Illinois, represented by Wooster (Station 2), Fort Wayne, and Freeport, respectively, form one group. The temperature in each of these States for the four years 1941–1944 was in general unfavorable for late blight. The 1942 season was probably the most favorable, and the 1944 season the least. These three States also reported the lowest losses.

Michigan, Wisconsin, Minnesota, North Dakota, South Dakota, and Iowa form another group. In these States the temperatures for the points chosen were much more favorable for the late blight organism. The favorable conditions were especially evident in 1942, 1943, and 1944.

Nebraska and Colorado fall into a third class because of the normally low rainfall and the use of irrigation for growing the majority of the crop. In Nebraska, it was only the early crop in the south central part of the State that was injured. Late blight was not found on the foliage in Colorado.

Probably the most significant fact apparent in the study of the data from each State is that in spite of much favorable weather in 1943 and 1944 there was a general reduction in losses suffered by the potato crop in the region.

The forecasting that was done throughout the season was based upon weekly weather reports but it will be observed that for the temperature and rainfall graphs in figure 1 and the data in table 2 monthly averages have been used. The use of weekly temperature and rainfall averages would have been desirable but would have been inconsistent with the amount of space which could be allotted for that purpose.

TABLE 1.—*The seasonal development of Phytophthora infestans and the practice of control measures in the Upper Mississippi Valley*

Year	Ohio	Indiana	Michigan	Illinois	Wisconsin	Minnesota	Iowa	N. Dakota	S. Dakota	Nebraska	Colorado
					Date of first field infection[a]						
1941	.....	.....	Sept. 3	.....	Aug.25	July 18	?	?	0	0	.....
1942	.....	Late Aug.	Aug. 12	Aug.	June 26	July 6	July 9	Aug. 5	July 27	June 21	.....
1943	.....	Late Aug.	July 9	Aug.	June 6	.....	July 23	Aug. 10	July 30	June 17	.....
1944	July	.....	Aug. 25	Late Aug.	July 11	July 9	July 1	Aug. 3	Not seen	Aug. 5	.....
					Percentage loss[b]						
1941	Tr.	.....	Tr.	.....	8	.....	Tr.	Tr.	0	0	.....
1942	5	Tr.	1	Over 3	25	30	33	25	30	1	.....
1943	Tr.	[b]	Tr.	2.9	11	3	16	5	13	5	.....
1944	Tr.	.....	Tr.	Tr.	12	10–15	1	1–5[b]	Tr.	Tr.	.....
					Time of greatest prevalence						
1941	Late	.....	Sept. 10	.....	Sept. 12–Oct. 5	.....	?	?	0	.....	.....
1942	do	Early Sept.	Aug. 20	Sept. 1–15	Aug. 25–Sept. 1	.....	.....	Aug.	Aug. 1–10	Aug. 1	.....
1943	do	Sept.	Sept.10	Mid-Sept.	Aug. 19–Sept. 11	.....	Aug. 15	Aug.	do	July 15	.....
1944	do	.....	Oct. 1	Late Sept.	Sept. 10–20	.....	Late Aug.	Sept.	.....	.....	.....
					Percentage growers dusting or spraying[c]						
1941	90	50	30	.....	18–100	85	5–50	2	24	50	25
1942	90	50	35	.....	20–100	85	5–50	10	25	50	25
1943	90	50	45	.....	30–100	85	15–90	40	17	75	25
1944	90	50	50	Over 2	36–100	85	20–90	60	8	80	25
					Amount (in 1000 lb) $CuSO_4$ used[d]						
1941	.....	.....	5200	.....	.....	.....	28,000	.....	52	2000	.....
1942	.....	.....	4500	.....	5–10% inc. over 1941	.....	25,000	.....	29	2000	.....
1943	.....	.....	5200	.....	45% inc. over 1942	.....	27,700	.....	23	3000	.....
1944	.....	.....	6000	.....	20% inc. over 1943	Inc. over 1943[d]	24,500	.....	62	3000	.....
					Number of spray or dust machines[e]						
1941	.....	.....	3500	.....	?	.....	10*	600	12	36	[e]
1942	.....	.....	3600	.....	31*– ?	.....	10	700	18	36	.....
1943	.....	.....	3800	.....	55 –40*	.....	16	1000	18	40	.....
1944	.....	.....	4000	.....	52 –48	[e]	20	1200	6	40	.....

[a] Late blight found at Marietta, Ohio, in 1944; ? indicates uncertain date or no information.

[b] In Indiana losses were severe on June plantings in 1943; in North Dakota there was 1 per cent loss on vines and 5 per cent loss on tubers in 1944.

[c] In Wisconsin and in Iowa the first number refers to small or home growers, the second number to large growers.

[d] In the Red River Valley of Minnesota sales were greater in 1944 than in 1943.

[e] An asterisk indicates power driven machines. In Wisconsin the first number refers to machines used by small growers, the second number to machines used by large growers. In Minnesota the large growers had dusters and six airplane dusters operated in the Red River Valley in 1944. In Colorado 20 per cent of the growers spray and 5 per cent dust.

The data in table 2 on the mean monthly temperatures for the four years show that the temperatures for June and September tend to be below 70° F. and the temperature was higher in June than in September. July was some-

TABLE 2.—*Mean monthly temperatures for 1941 to 1944 inclusive, for June, July, August, and September for eleven states*

State	Station	Year	Mean monthly temperature (°F.)			
			June	July	August	September
Ohio	Wooster 2	1941	69.6	73.5	69.5	67.4
		1942	69.8	73.6	70.6	64.4
		1943	73.6	73.2	71.0	60.8
		1944	72.8	73.1	72.4	63.1
Indiana	Fort Wayne	1941	69.0	74.25	73.25	68.6
		1942	71.0	73.75	70.75	63.4
		1943	73.0	72.75	72.0	59.5
		1944	71.5	74.5	73.6	65.0
Illinois	Freeport	1941	69.6	74.0	72.6	66.4
		1942	68.8	72.6	69.9	60.8
		1943	71.6	73.7	72.0	58.3
		1944	71.4	71.0	71.3	64.6
Michigan	East Lansing	1941	68.1	71.1	68.4	64.4
		1942	67.0	70.2	67.8	59.4
		1943	69.6	70.4	68.6	57.5
		1944	68.4	70.4	71.0	62.1
Wisconsin	Antigo	1941	66.1	69.7	66.0	60.8
		1942	63.0	66.6	65.7	56.3
		1943	66.7	69.8	67.4	53.8
		1944	65.6	68.0	68.4	59.2
Minnesota	Albert Lea	1941	69.0	73.8	73.3	63.6
		1942	66.0	70.7	69.4	56.9
		1943	69.1	73.4	70.6	56.8
		1944	68.5	69.1	69.8	60.6
North Dakota	Grand Forks	1941	64.8	71.4	66.8	56.0
		1942	61.8	71.8	67.1	57.6
		1943	61.1	66.4	65.6	54.0
		1944	64.2	68.2	66.4	56.2
South Dakota	Watertown	1941	66.4	72.7	71.7	.....
		1942	64.4	69.5	68.5	53.9
		1943	66.3	74.3	70.5	56.3
		1944	66.1	69.6	67.7	58.3
Iowa	Forest City	1941	69.0	73.4	73.4	64.6
		1942	67.0	71.1	69.8	58.2
		1943	69.5	73.4	70.8	57.4
		1944	70.75	70.75	71.2	64.0
Nebraska	Grand Island	1941	70.0	77.6	76.6	66.0
		1942	70.4	78.6	74.4	61.4
		1943	71.0	79.0	79.0	63.6
		1944	71.9	76.5	75.6	65.6
Colorado	Greeley	1941	65.4	72.0	70.0	58.6
		1942	65.7	73.0	70.2	60.0
		1943	65.3	75.1	74.2	61.2
		1944	66.6	71.8	72.8	61.7

[a] An asterisk indicates power driven machines. In Wisconsin the first number refers to machines used by small growers, the second number to machines used by large growers. In Minnesota the large growers had dusters and six airplane dusters operated in the Red River Valley in 1944. In Colorado 20 per cent of the growers spray and 5 per cent dust.

what warmer than August. When the temperature conditions in June and July were favorable for the development of the pathogen, 70° or below, the disease became prevalent. Its subsequent destructiveness is influenced favorably or adversely by the temperature in August. September was al-

ways sufficiently cool to permit the organism to develop freely, providing ample susceptible foliage existed. In other words, the conditions in June and July govern the initial stages of the pathogen and those in August the final stages.

DEVELOPMENT OF THE PATHOGEN AND CONTROL PRACTICES

According to the data recorded in table 1, the late blight pathogen most often made its first appearance in June and July except in North Dakota, Illinois, Indiana, and Michigan where it was most often first seen in August. In all States it was recorded most prevalent in August or September except in Michigan where in 1944 it did not become most prevalent until October. The late blight disease was least destructive in 1941 and most destructive in 1942. In 1942 the estimated loss was about 25,586,000 bushels. In 1941 the only State that reported more than a trace of late blight was Wisconsin which recorded an estimated 8 per cent. In 1943 nine States reported an estimated loss of about 6,164,000 bushels. Just how much the spraying and dusting program reduced the loss is not apparent from the data in hand, but the sharp increase that took place in control practices doubtless had a strong retarding effect on the development of the pathogen.

The losses in 1944 ranged from a trace to 10 to 15 per cent. The only States that experienced important losses were Wisconsin with 12 per cent, Minnesota with 10 to 15 per cent, and North Dakota with one per cent foliage loss and 5 per cent tuber rot. It is impossible to convert these losses for 1944 into bushels because yield data are not at hand, but it is probable that the loss from late blight over the region in 1944 was considerably less than in 1942.

The most significant result apparent in the data shown in table 1 was the increase in control practices. In most of these States there was a sharp increase when 1941 and 1942 are contrasted with 1943 and 1944. The number of dusters and sprayers doubled (600 to 1,200) in four years in North Dakota. The increase in machines was sharply upward also in several of the other States, as Wisconsin, Minnesota, Michigan, Iowa, and Nebraska. In Minnesota, six airplane dusters were in operation in 1944.

The amount of copper sold in different forms seemed to increase from year to year but this probably is a less reliable criterion of the control effort than the number of sprayers and dusters. In most cases it was difficult to obtain complete information relating to the amount of fungicide used.

This vigorous effort in combatting the late blight pathogen in the region, without doubt, materially retarded the organism in 1943 and 1944 and resulted in the saving of several million bushels of potatoes.

Ohio

The choice of data that would represent a typical Ohio potato region was difficult because there were a number of rather widely separated areas in which potatoes were grown. Obviously the weather data of all sections

could not be graphically shown. Wooster was chosen because it probably represents one of the largest potato growing areas and also because there are two weather recording stations. The temperature and rainfall data for Stations 1 and 2 were somewhat different. Station 2 recorded the temperature about 2 degrees higher than Station 1 throughout the four-month period under consideration. Station 2, recording the higher temperatures, will be used in this study.

There was only a trace of late blight in 1941. The temperature during June, July, and August was probably too high to permit abundant development of the pathogen since it was approximately 70° F. or above for the entire period.

In 1942 the late blight loss was recorded as 5 per cent although the temperature condition was approximately the same for June, July, and August as in 1941 (1942 temperatures were less than a degree higher than 1941) when only a trace of late blight was observed. It is significant that the rainfall was much lower in 1942 than in the previous year.

In 1943 and 1944 only a trace of late blight was observed in the State. The temperatures for the first three months of the growing season of each year were too high to permit extensive development of the pathogen.

Indiana

Late blight was not recorded in Indiana in 1941. The temperatures for June, July, August, and September for the Fort Wayne region were 69.0°, 74.25°, 73.25° and 68.6° F., respectively, which means that for most of the time the temperature was near or above the maximum for the development of the late blight pathogen. During the same months the rainfall was + 0.08 inches above and – 1.76, – 0.60, and – 2.64 inches, respectively, below the normal. The stations at Indianapolis, Terre Haute, and Evansville recorded higher temperatures than the one at Fort Wayne, with the rainfall about the same. Hence the weather for this portion of the State was probably too warm and dry for the late blight organism.

Records for 1942 present a picture different from that for 1941. Late blight was reported in the northern part of the State in late August and was most prevalent in the early part of September. The mean temperatures for June, July, August, and September were 71°, 73.75°, 70.75° and 63.4° F., respectively. The continuous high temepratures for the first three months of the growing season were not favorable for the extensive development of the pathogen, although the rainfall was above normal during this period.

In 1943 late blight also occurred, but the injury to the crop was slight. The disease was most prevalent in September, with an estimated loss of 0.2 per cent (Plant Disease Reporter Supplement 147, p. 177, 1944). The mean temperatures for June, July, and August were 73.0°, 72.75° and 72.0° F. The September temperature dropped to 59.5°. The rainfall in June, July, and August was – 1.01, + 0.97, and + 0.57 inches, respectively.

No late blight was found in 1944. The temperature during the first three

growing months was continuously above 70° F. The rainfall was below normal during June and July, slightly above in August, and −2.1 inches in September. The high temperature and generally low rainfall prevented the development of the late blight organism.

Illinois

Late blight was not observed in Illinois in 1941. The temperatures at Freeport for June, July, August, and September were 69.6°, 74.0°, 72.6° and 66.4° F., respectively. The temperatures for the first three months, especially July and August, were sufficiently high to inhibit the growth of the pathogen. During the same months the rainfall was +0.08 inches above normal for June but below normal for the balance of the season. The high temperature and low rainfall undoubtedly prevented the late blight organism from developing.

The first reported occurrence of late blight in 1942 was in August. The estimated loss was reported as greater than in 1943 (the loss in 1943 was reported as 2.9 per cent). It is reported that late blight was most prevalent during the first half of September. The temperature in June, August, and September was below 70° F., while in July it was 72.6°. The rainfall in July and August was above normal and in June and September, below. The favorable temperature in August and September, coupled with deficient rainfall for the same period, permitted a limited development of the pathogen.

In 1943 the disease was first reported in August and was most prevalent in the first half of September. The temperature was high (above 70° F.) during the first three months and very low in September (58.3°, which was 5.0° below normal). The rainfall fluctuated from above to below normal in alternating months, beginning with a +2.53 inches above normal in June. The temperature range for the season was unfavorable for the development of the pathogen, except in September.

In 1944, there was only a trace (estimated 0.8 per cent) of late blight, which was first reported in late August. The mean temperature for the first three months was approximately 71° F., dropping to 64.6° in September. The rainfall was high in July (+1.08 inches) and below normal in June, August, and September. The weather conditions were most favorable for the development of the late blight organism at Freeport, Illinois, in 1944.

Michigan

Late blight occurred in Michigan in each of the years 1941 through 1944. East Lansing weather data for 1941 (Fig. 1) show the temperature for June, August, and September to be below 70° F. Rainfall for the same three months was above normal. Temperature in Northern Michigan (Onaway) was slightly lower than at East Lansing with approximately the same amount of rainfall. July was warm and dry in both regions. In Western Michigan (Ironwood) the temperature was approximately that of Onaway, but rain-

fall in July was heavier. The first late blight found in 1941 was in Emmet County, about 50 miles west of Onaway.

In 1942 the South-central Michigan weather was somewhat more favorable for late blight than 1941. The temperature during June and July was 67.0° and 70.2° F., respectively, with rainfall above normal for July. Temperature at Onaway was 3 to 4 degrees lower but there was less rainfall. Western Michigan temperature was about the same as that of the northern part of the State, but there was much more rainfall. For example, Ironwood received 10.12 inches in July; Iron Mountain 5.92 inches, compared to 4.33 inches at East Lansing. Late blight was first reported in Northern Michigan (point not specified) August 12. The total loss for the State was estimated as one per cent.

In 1943 East Lansing temperatures were 70° F. or below for the summer, except for a July mean of 70.4°, with June and July wet. Northern Michigan temperatures were 3 to 4 degrees lower on the average, but with lower rainfall for June and July. Somewhat more rain fell in Northern Michigan during August and September than in the East Lansing area. Western Michigan was a little warmer than Northern Michigan, with more rainfall during June, July, and August. The first report of late blight was July 9 in Western Michigan in Menominee County. This early occurrence would be expected, as weather for June and July was more favorable for late blight in Western Michigan than near East Lansing. Loss for the season was estimated at a trace.

In 1944 the weather for the State was somewhat more uniform than in the two previous seasons. Late blight was first reported in Houghton County, Western Michigan, on August 25. Dr. Muncie reported as follows: ". . . late blight in August and with continued precipitation beginning early in the month with high day temperatures and cool night temperatures late blight became established and caused considerable damage before the crop was harvested in late October." Late blight appeared in Presque Isle County in September and October. The loss to the Michigan crop was less than one per cent.

It may well be that the vigorous control program carried on every year in Michigan materially retards the development of the pathogen, especially when the temperature in June and July is below the maximum for the development of the parasite. The mean temperature for July was always slightly above 70° F. Michigan growers operate 3,500 to 4,000 sprayers and dusters.

Wisconsin

Late blight was destructive in Wisconsin from 1941 to 1944 inclusive. The loss, estimated at 4 per cent, in 1941 was less than for any of the three following years. The disease was first reported August 23 on the late crop in Waupaca County.

The monthly mean temperatures at Antigo for June, July, August, and September of 1941 were 66.1°, 69.70°, 66°, and 60.8° F., respectively. The

rainfall in June and July was low, −2.74 inches and −2.13 inches below normal, while in August and September the rainfall was +8.77 and 2.97 inches above normal. The unusually low rainfall in June and July may well have retarded the development of the pathogen.

The late blight losses in 1942 were high, estimated at 20 per cent in the field and 5 per cent in storage. This loss was over five times that in 1941. The disease was reported in the State about two months earlier in 1942 than in 1941, which meant the pathogen probably had a much longer period in which to develop. It was most prevalent and destructive in late August. The temperature during the growing season was prevailingly lower than in 1941 for June to September, being 63.0°, 66.6°, 65.7°, and 56.3° F., respectively, and the rainfall higher during the early part of the season, being only −0.52 and −0.25 below normal for June and July. It should be emphasized that the mean temperature throughout the season was very favorable for the development of the pathogen.

There was only a 5 per cent loss in the field and about a 6 per cent loss in storage in 1943. The field losses were much less than in 1942, but the storage rot losses were about equal. The disease was first reported on June 6 in Langlade County on the late potato crop. The disease was most prevalent in late August and early September. The temperatures for June, July, and August were +2.8°, +1.3°, and +1.9° above normal. On the other hand, September was cool, with −4.5° below normal. The rainfall was above normal during the first three months and below in September. The temperature conditions in 1943 were much like those of 1941, being less favorable for the pathogen during the first three months of the growing season than during the same period of 1942. The late blight losses were estimated at 4 and 5 per cent for 1941 and 1943, respectively.

In 1944 the late blight estimated loss was only 2 per cent in the field, but much higher in storage, estimated at 10 per cent. The disease was first reported June 11 in Langlade County, but it became prevalent only in September at about harvesting time. The temperature for the first three months was somewhat higher than 1942 and lower than 1943. It was significant that the August temperature was higher than for any of the three previous years. The rainfall was low in July (−1.4 inches), high in August (+3.5 inches), and low in September (−1.26 inches). The temperature curves for 1942 and 1944 parallel one another with only about a degree difference, conditions that certainly were favorable for the development of the pathogen throughout the season. It is believed that the vigorous control program in effect in 1944 may well have saved thousands of bushels of potatoes.

Minnesota

The potato growing areas of Minnesota are rather widely separated and for this reason no one station's weather data can be used to represent the State as a whole. In this report the temperature and rainfall recorded for Albert Lea were selected since the Red River Valley area could be considered with the North Dakota conditions.

In 1941 the temperature during June was favorable for the development of late blight pathogen around Albert Lea. In the Red River Valley the temperature and rainfall were favorable during June. The first late blight was reported at Brooklyn Center on July 18, but no estimated loss for the State is available.

In 1942 the weather at Albert Lea was even more favorable for late blight. In the Red River Valley there was generally heavy rain, with the mean monthly temperature below 70° F. during June, August, and September and only 0.7° above in July. The first late blight was reported at Hollandale, near Albert Lea. Late blight apparently was general in the State because the estimated loss for the State was 30 per cent.

The temperature was in general less favorable for late blight in 1943 than in 1942. There was less rain in the vicinity of Moorhead and Crookston in the Red River Valley than in the Hollandale area for the same periods, but there was enough rain to provide favorable conditions for the pathogen and some late blight occurred, although the date of first appearance is not available. Loss for the State during 1943 was estimated at 3 per cent.

In 1944 the weather at Hollandale was favorable for late blight for much of the season. The temperature was low during June, July, and August with ample rainfall. At Crookston the temperature was below 70° F. for much of the time but the rainfall was also low. The late blight pathogen was first reported in cull piles at Hollandale but the first field report was at East Grand Forks, July 9, about 200 miles north. The estimated crop loss for the season was between 10 and 15 per cent.

It should be pointed out that in 1941 and 1943 the temperatures were higher during June, July, and August than during the same months of 1942 and 1944 (monthly mean temperatures at Albert Lea). The estimated late blight loss was much less in 1941 and 1943 than in 1942 and 1944.

North Dakota

The temperature and rainfall records at Grand Forks for the four years for North Dakota are in figure 1. The loss in 1941 was recorded as only a trace. The temperature was unfavorable in July but favorable in August and September.

In 1942 the loss was serious, amounting to 25 per cent of the crop. The first report of blight occurrence was on August 5 in Grand Forks County and later it was reported in Walch, Sargent, and Richland counties in the Red River Valley. The temperature was favorable throughout the growing season. The only month when the temperature was at all unfavorable was July when it was above the maximum. The rainfall was below normal in June, July, and September, but above normal in August.

The temperature was generally lower in 1943 than in either 1941 or 1942. The rainfall was very low in August and September, but it was above normal in July. Late blight was first observed on August 10 and was estimated to have caused a 5 per cent loss. It is believed that the very dry

condition in the last half of the growing season adversely influenced the development of the late blight organism.

The weather conditions in 1944 were very different from those in 1943. Instead of being dry during the last half of the season it was very wet. The rainfall in August was 12.16 inches. The temperature was favorable throughout the growing season and late blight was prevalent beginning August 2 in Walch, August 8 in Thraill, August 11 in Cass, and August 23 in Pembina counties. The estimated loss was one per cent on the foliage and 5 per cent in storage. Dr. Brentzel advised by letter that, because of severe hopper damage, most of the vines in these areas were dead and dried by the time the heavy rains fell in August, thus the lack of abundant susceptible foliage prevented the occurrence of a late blight epiphytotic.

South Dakota

Late blight occurred in South Dakota in 1942 and 1943, but not in 1941 and 1944. The temperature at Watertown in July and August was distinctly unfavorable in 1941. The same can be said of the rainfall for these two months.

In 1942 the temperature was generally below 70° F. and late blight occurred in destructive form in the State. It was estimated that the loss for the State was 30 per cent. The disease was first discovered in Deuel and Brookings counties on July 27.

The weather for the growing season in 1943 was warmer than in 1942. The temperature was unfavorable for the development of the late blight pathogen in July and August, with the August mean only +0.5° above the maximum for the pathogen. In spite of this unfavorable temperature period, considerable late blight occurred. The loss was estimated at about 13 per cent.

The 1944 season was much like 1942 from the standpoint of temperature and rainfall. The mean temperature throughout the growing season was below 70° F. in each year. The rainfall in 1944 was low in June and July and only slightly above normal for August and September. The late blight loss was, according to estimates, only a trace for this season. The difference in the development of the late blight pathogen in 1942 and 1944 may have been due to the dry June and July in 1944 which prevented the initial development of the pathogen in the potato fields.

Iowa

Late blight has appeared in Iowa in each of the last four years. In 1941 late blight was not observed until in September, when it was collected on tubers in two different counties. Data in hand for 1941 indicate that late blight was neither prevalent nor destructive. The temperature for 1941 during July, August, and the early part of September was above that permitting rapid development of the pathogen. The last half of September, on the other hand, was below 70° F. and favorable for the development of

the pathogen. This unfavorable temperature condition for July and August probably explains why only a small amount of late blight was present in 1941. The rainfall in these two months was low (July +1.1 inches and August −2.2 inches) while in September (+3.4 inches) it was high.

In 1942 the late blight picture and the temperature and rainfall conditions were markedly different from those in 1941. Late blight was prevalent and destructive. In fact, it was estimated that 33 per cent of the potato crop was destroyed. The disease was first found on July 9. The temperature was below 70° F. in June, August, and September, and in July it was only slightly above. The rainfall was rather low throughout the whole period. There was, however, enough rainfall so that the crop never suffered from lack of moisture. This is apparent in that, in spite of the heavy late blight loss, Iowa produced 120 bushels per acre.

The estimated crop loss in 1943 was 16 per cent, about half of that in 1942. The temperature during June, July, and August was higher than in 1942 and July was 3.4 degrees above the maximum for the development of the pathogen. September was cool with little rainfall. Late blight was first found on July 23, about two weeks later than in 1942, and the disease was most prevalent on the vines in late August.

There was less late blight in 1944 than in either 1942 or 1943. The loss in 1944 was estimated as only one per cent. The temperature during June, July, and August was just above the maximum for the development of the pathogen. The temperature conditions in 1944 were more like those in 1941 than either 1942 or 1943. The rainfall was generally high throughout all four months.

The late blight disease during 1941 to 1944 inclusive was most destructive in 1942 and 1943 and least in 1941 and 1944. When the temperature was generally above 70° F. the pathogen was much less destructive than when it was below. The rainfall was lowest in 1942 and highest in 1944. There seemed to be little relation between rainfall and the prevalence and destructiveness of the late blight pathogen.

Nebraska

Late blight was not observed in Nebraska in 1941, although the temperature and rainfall conditions were favorable in June for the development of the pathogen on the early crop. An early crop, grown in the vicinity of Grand Island, is normally harvested in July.

In 1942 late blight was observed at Wood River, near Grand Island, in Hall County, on June 21 on the early crop. The mean temperature for June was 70.4° F. and the rainfall was 7.7 inches. This condition of below normal temperature (−1.6°) and above normal rainfall (+3.65 inches) was favorable for the limited development of the pathogen on the early crop.

The mean temperature in June of 1943 was 0.6° higher than 1942 and the amount of late blight was 5 per cent, some higher than in the previous year. The disease was most prevalent about the middle of July, at harvest time.

The weather condition in June, 1944, was much like that in 1942. The temperature was 71.9° F. and the rainfall 5.44 inches. The late blight disease was very limited, a trace having been observed on August 5 in only one field at Cozad in Dawson County, about 75 miles west of Grand Island.

In Nebraska the late blight situation was very different from that in most other States in the region, because only the early potato crop on mineral soil was diseased. Therefore, it is only the weather condition in the earlier part of the growing season, May and June, that influences the development of the pathogen and the regional forecasting service would not operate early enough to serve that area effectively.

Manitoba

In the absence of temperature data for the Province of Manitoba, no attempt will be made to correlate the temperature and late blight prevalence. The following extract from a report by Dr. J. E. Machacek is an excellent summary of the prevalence and destructiveness of late blight in Manitoba during the four years under consideration:

"In 1941, late blight appeared in Manitoba for the first time since 1928. Rainfall was extremely heavy from August 15 to September 30 with but very little sunshine and many potato fields were covered almost continuously with water. The greatest losses occurred north of Winnipeg but the disease apparently did not spread very far from the vicinity of this city. Early varieties, such as Warba, escaped tuber infection, but in later varieties, such as Irish Cobbler, as much as 7.5 per cent of the tubers in a field were infected.

"In 1942, late blight was again prevalent in the Red River Valley around Winnipeg and in some fields it was severe. The extent of tuber-rotting was difficult to determine because early, severe frost damaged a considerable percentage of undug tubers in September and the occurrence of secondary rots obscured decay from the late blight fungus. In general, the weather during late summer was similar to that in 1941.

"Following a moist, cool July, in 1943, late blight appeared in the Winnipeg area during the early part of August, and spread rapidly for a few days. Its progress was checked toward the end of August and in September by a period of dry weather. Severe tuber-rotting occurred, however, in some areas north of Winnipeg, and some damage occurred in western and northwestern Manitoba in fields 150 to 200 miles from Winnipeg.

"In 1944, the weather was very moist and moderately warm during June, July, and August. Late blight was first found in the Winnipeg area in a Victory Garden on July 15 and within a few days it could be found with ease in most of southern Manitoba. By September, the disease had done so much damage that a great many fields were left unharvested. During autumn and winter, rotting tubers were received from practically all agricultural portions of the Province, and also occurred frequently in tubers sold in Winnipeg by retail grocers. The severity of the late blight epidemic in 1944 appeared to be the greatest in the history of the Province.

"The rapid spread of the disease in Manitoba from 1941 to 1944 can be attributed to three principal factors: (1) the unusually moist weather, (2) the unfamiliarity of Manitoba potato growers with the disease during 1941 and 1942, and (3) the current unavailability of spraying materials and equipment."

FORECASTING LATE BLIGHT

Reports from the Sub-committee of the War Service Committee of the Upper Mississippi Valley Plant Pathologists were sent to the chairman at weekly intervals and the data compiled and sent out to pathologists and others interested in potato growing.

In some of the States, seed infected with *Phytophthora* was actually planted so as to afford information on the time of occurrence of the disease. In most cases, however, the development of the pathogen was watched in field plantings and on cull piles near warehouses and on dump piles on the outskirts of towns and villages. The following are a few of the forecasts that were made for 1943. The first forecast to the committee for distribution and use was on June 17, with eight States reporting: North Dakota, Michigan, Wisconsin, Minnesota, Nebraska, South Dakota, Colorado, and Iowa. The forecast was as follows:

"From the standpoint of moisture and temperature, the conditions seem generally to be favorable for the development of the early stages of an outbreak of late blight. In two States the organism has been found fruiting in late gardens and dump heaps. Barring a very sharp and sudden rise in temperature and drop in rainfall for Iowa, late blight will appear in our fields in Early July."

Late blight was found on July 23. The area of vines diseased in the two fields where the disease was first found already comprised several acres, so it is safe to assume that the initial stages of the spread of the pathogen existed from two to three weeks earlier. The forecast on June 17 came true.

The following week, June 26, this forecast was formulated from the data from the same eight States that reported on June 17:

"The late blight organism is developing true to form, and has made a beginning in several places. Information in hand justifies the prediction that the early stages of foci of infection exist. Only a sharp rise in the temperature can stop the organism's increase and spread. Fortunately, the temperature during the past two weeks has been generally upward. Watch the temperature, it is much more damaging to the organism than rainfall."

The next announcement was made on July 19, based on the data supplied by Iowa, South Dakota, Minnesota, Wisconsin, Nebraska, and Michigan. The forecast was as follows:

"The over-all picture is still dark, and conditions are favorable for an epiphytotic over most of the Upper Mississippi Valley. The only bright spots that developed in the first half of July were the high temperatures

in South Dakota and Minnesota. In spite of all this it should be emphasized that a couple of weeks of favorable weather now can induce a widespread epiphytotic. The vines are beginning to close the rows, affording shade and slow evaporation, conditions that favor *Phytophthora*. The only safe thing to do is to keep the sprayers going. If the vines need protection from the tractor wheels, buy or devise vine lifters and keep going."

On July 27 came this warning: "The situation will be serious if a few cool days come. Present weather conditions are hot and dry. With late blight present in fields in North Central Iowa and the weather such as it is in that area, potato districts further north, including the States of Minnesota, Wisconsin, and the Dakotas, are liable to late blight losses unless the temperature rises very sharply and remains well above normal for the balance of the growing season."

North Dakota, South Dakota, Minnesota, and Wisconsin experienced the expected losses. The late blight disease even occurred in the Canadian provinces, although not in destructive form, except in Manitoba.

The last forecast for the season was disseminated on August 4 and reads: "If we can avoid late blight losses we will harvest the biggest crop produced during the last two decades. The early potato crop will be marketed with little loss from late blight, but this will not be true of the late crop. Our early crop always escapes. It is now clear that late blight will do considerable damage to the foliage as the season advances and there will be considerable tuber rot unless the weather turns hot and dry right away. The potato crop in most areas was planted later than usual, which means that it will go into the fall in a vigorous growing condition with lots of foliage, affording an opportunity for a large spore load to sift down into the soil. No amount of spraying can stop this."

The data in table 1 show the following losses in percentage of each State's crop: South Dakota 13, North Dakota 5, Nebraska 5, Iowa 16, Minnesota 3, Wisconsin 11, Illinois 2.9. The forecast of August 4 came true. The basis of the forecast was the favorable weather for the development of the pathogen in June and July.

In 1944 the first forecast was issued on June 5 and read as follows: "Every indication at the present tells us to keep a 'weather eye' on the late blight situation." The prediction of June 5 was strongly supported in the communication of June 26: "Weather conditions have again been favorable for the development of *Phytophthora infestans*. The temperature was slightly above normal except in North Dakota. The rainfall, on the other hand, was low except in Illinois, Wisconsin, Minnesota, and South Dakota."

By July 17 the late blight picture was well outlined, as manifested by this statement: "By this time it is perfectly clear to all of us that late blight, if conditions remain favorable, will cause heavy losses in potatoes that are not sprayed. Fortunately through the splendid work that has been done much spraying has been and is being done. I predict little damage generally in the intensive potato growing regions."

On July 24 came another reminder to the effect that "we must not relax our vigilance for there is still time for the pathogen to cause serious loss."

The situation as of August 14 was as follows: "This season has been an extremely interesting one from the standpoint of late blight. You will recall we started the season with the pathogen general in our seed, which explains the 'popping up' of local epiphytotics in the field from Ohio to Nebraska and from Iowa to Manitoba. Except that the temperature remained close to the upper limit for the development of the late blight organism, we would have experienced a bigger fight in protecting our crop."

The forecast of July 17 was borne out by the following losses: in Wisconsin 12 per cent, Minnesota 10 to 15 per cent, North Dakota, on the vines one per cent and on the tubers 5 per cent. Favorable temperatures in June and July in the States named was the basis for the forecast.

CONCLUSION

Thus, in conclusion, it is possible to summarize by stating that, given the weekly temperature and rainfall of the potato growing areas and assuming that sources of inoculum exist near the potato fields, one can rather accurately predict the prevalence and destructiveness of the late blight pathogen throughout the growing season.

PHYTOPATHOLOGICAL NOTES

A Diplodia Associated with Concealed Damage in Peanuts.—Concealed damage is the name given to an internal deterioration of peanut seed. In the early stages of the disease there is a small dirty white to light yellow spot on the inner face of the cotyledon. As the disease progresses the discoloration becomes more pronounced until the entire embryo is blackened and thoroughly permeated with fungal hyphae, and the cotyledons become rancid. A dense mycelial mat often is between the cotyledons. Only in the last stages of deterioration is the damage evident in unbroken seeds.

The cause of the disease has not been conclusively established. Higgins[1] isolated *Rhizoctonia, Penicillium, Rhizopus,* and *Sclerotium bataticola* from seeds with concealed damage and concluded that these soil-inhabitating fungi were responsible for the disease. Results obtained during the fall of 1944 at the Alabama Agricultural Experiment Station do not support this conclusion.

Samples of peanuts were collected from twelve widely separated fields throughout the principal peanut-growing region of Southeast Alabama. All seeds having concealed damage were separated from each sample for isolation of the associated microflora. Disinfecting solutions used were 1–1,000 mercuric chloride, silver nitrate, and 0.5 per cent sodium hypochlorite. Potato-dextrose agar acidified with lactic acid, beef-extract agar, and Czapek's solution agar were used to provide media varying in nutrients and hydrogen ion concentrations. Over 1,200 seeds from the twelve samples have been studied.

Regardless of the method of sterilization or the medium used, the predominant organism obtained was a *Diplodia.*[2] This fungus was obtained from 65 per cent of all seeds plated and constituted approximately 95 per cent of all isolates. Other fungi obtained (5 per cent of the isolates) were *Sclerotium bataticola, Fusarium spp., Aspergillus, Penicillium,* and *Rhizopus;* and bacteria also were isolated.

The frequency with which this *Diplodia* is recovered from damaged seed is strong evidence that it is associated with the disease.—COYT WILSON, Alabama Agricultural Experiment Station, Auburn, Alabama.

Galls on the Roots of Citron-Watermelon Hybrids.—During the course of studies on the Fusarium wilt disease of watermelons at Leesburg, Florida, it was a routine procedure to pull all plants at the end of the season and observe Fusarium wilt injury on the roots. Included in the 1934 trials were several F_1 hybrids from crosses of watermelons on three strains of African citron obtained from the Iowa Agricultural Experiment Station. When these plants were pulled peculiar galls were observed on the roots of many

[1] Higgins, B. B. "Concealed Damage" of runner peanuts. Georgia Agr. Exp. Sta. Press Bul. 536. 1944.

[2] Tentatively identified as *Diplodia theobromae* (Pat.) Nowell, by Dr. J. A. Stevenson, United States Department of Agriculture.

of them, particularly on those of three hybrids designated as 427, 430b, and 431. There were no plants of the citron parents in the field, but similar structures were observed later in the same year on the roots of volunteer citron plants on the Experiment Station Farm at Gainesville. Galls were observed on the citron hybrids again in 1935, which was the last year they were planted and none of the galls have been observed since that year. Since these galls were entirely different in appearance from galls induced by nematodes or the crown-gall organism, the observations on them are recorded here.

FIG. 1. Roots of citron-watermelon hybrid showing variations in the unusual type of gall.

The galls were most evident on the larger roots but they were also observed on the smaller ones. There was no swelling of the large roots on which the galls occurred, and the growths appeared to be appended to the roots by definite stalks which on the larger galls were comparatively inconspicuous. It is possible that these pedicel-like structures were merely portions of small lateral rootlets. In any event, this characteristic of the galls was a distinct point of difference from the galls induced either by *Bacterium tumefaciens* Smith and Towns. or by the root-knot nema, *Heterodera marioni* (Cornu) Goodey.

The galls in the early stages of development were glistening white. This character was less conspicuous later, though still apparent between the fine network of growth cracks that covered the surface of the older growths. In

somewhat larger galls the surface became darkened and slightly scurfy, sloughing off to again expose the fresh sub-surface region of active growth. The largest galls were inclined to be tuberculate and divided, apparently as a result of the irregular enlargement of limited portions of the surface of the growth. This often resulted in a dense cauliflower-like structure that is evident in some of the galls shown in figure 1. Another characteristic of some of the growths was the proliferation of roots around the gall.

Bacteria were numerous in intercellular pockets throughout the superficial layers of the galls. Occasionally nematodes were observed but not consistently or abundantly enough to suggest a causal relationship. A single inoculation series was carried out with cultures of bacteria isolated from the galls, but because galls appeared on the check plants as well as on those that had been inoculated the test was of no value and opportunity for further work has never arisen.—M. N. WALKER, Florida Agricultural Experiment Station, Gainesville, Florida.

REPORT OF THE SECOND ANNUAL MEETING OF THE POTOMAC DIVISION OF THE AMERICAN PHYTOPATHOLOGICAL SOCIETY

The second annual meeting of the Potomac Division of the American Phytopathological Society was held February 20 and 21, 1945, at the Plant Industry Station, Beltsville, Maryland. Officers elected for 1945 were T. F. Manns, President; E. E. Clayton, Vice-President; V. F. Tapke, Secretary-Treasurer; and R. J. Haskell, Councilor. Plans are going forward for a one-day field meeting at the Plant Industry Station during the latter part of August.

ABSTRACTS OF PAPERS PRESENTED AT THE SECOND ANNUAL MEETING OF THE POTOMAC DIVISION

Light and Composition of Media as Factors Inducing Sporulation in Strains of Alternaria solani. BEECHER, F. S. The fungus, *Alternaria solani*, which attacks both tomatoes and potatoes, ordinarily sporulates only sparingly, if at all, in artificial cultures. Various workers have induced sporulation by wounding, by scraping, or by irradiation of cultures with ultra-violet light. Considering light as a possible essential factor, closed Petri-plate cultures were exposed to various types of illumination. Sunlight in the greenhouse gave fair sporulation on some media, but was too variable and the heat often too intense. A 300-watt Mazda lamp was without effect. Twenty-four-hour exposure, close to a 3-tube (40 watts each) fluorescent lamp, gave moderate sporulation. Six- to eight-day-old cultures, irradiated under an S–1 sun lamp for 30 minutes or longer at a distance of 30 to 32 inches, sporulated abundantly, especially on bran-extract medium (1 oz. of bran per l., boiled 10 or 15 min., strained and decanted; 10 cc. per l. of a 5-per cent solution of ferric chloride; 2 per cent of agar). This extract, alone or combined with juice of green or ripe tomato fruits, gave varying results with different strains of *A. solani*. Plates kept in darkness showed no sporulation, except in rare instances. *Alternaria tomato* gave little if any response to irradiation, but eventually sporulated slowly in the laboratory in light or darkness. (Division of Fruit and Vegetable Crops and Diseases, Bureau of Plant Industry, Soils, and Agricultural Engineering, Agricultural Research Administration, U. S. Department of Agriculture.)

Chemical Soil Treatments for Disease and Weed Control in Tobacco Plant Beds. CLAYTON, E. E., J. G. GAINES, T. E. SMITH, AND T. W. GRAHAM. Treatments with uramon (urea), 1 to 1½ pounds per square yard, were effective against weeds, black root rot, and root knot. Cyanamid (calcium cyanamide) was effective against weeds but not against black root rot or root knot. Chemicals were applied September–November, and tobacco seed was sown the following January–March. Among other materials tested, D–D mixture gave excellent root knot control but did not destroy weeds or black root rot. The best chemical treatment in 1944 was 1 pound of uramon and ½ pound of cyanamid per square yard. This gave 95 per cent weed control, excellent root knot control, and an average of 21 transplants per square foot. The corresponding yields of plants from uramon and cyanamid used alone were 13 and 15. The better chemical treatments have been superior to steam sterilization with respect to disease control and yield of plants, and inferior with respect to weed control. Best results with chemical treatments have been obtained on light, sandy soils.

Pre-storage Treatments for Seed Sweetpotatoes. COX, CARROLL E., AND W. F. JEFFERS. Maryland Golden sweetpotatoes were treated before curing and storage for the purpose of reducing losses from decay and preventing spread of diseases during storage. Immediately after digging, potatoes were washed in water and dipped one minute in 4-oz.-per-gallon solutions of borax, Spergon, and calcium propionate (Mycoban); the same materials in five per cent colloidal silica suspension; and the silica suspension alone. Both washed and unwashed potatoes were included as checks. The potatoes were cured for 12 days at 75–78° F. and a relative humidity of 95–99 per cent and stored at 55–60° F. and a relative humidity of 80–85 per cent. Loss in weight and percentage of rot were determined soon after curing and again after 3 months' storage. Sweetpotatoes treated with borax, borax and silica suspension, and calcium propionate lost significantly more

weight and contained a higher percentage of rotted potatoes than those treated with Spergon, Spergon and silica suspension, silica suspension alone, or either of the checks. None of the treatments significantly controlled storage rots. When bedded Spergon-treated potatoes produced sprouts several days earlier than other treatments.

Thielavia terricola from Cotton Fabric and from Soils. DIEHL, WILLIAM W. *Thielavia terricola*, hitherto with no known conidial stage, is shown to bear amerosporous conidia on germ tubes shortly after germination of the ascospores, but no conidia have been detected in older cultures. The history of the fungus, as shown by specimens and by cultures isolated from soils, from plant roots, and from deteriorated cotton fabrics, reveals a wide distribution in nature. These records, together with the fact that in pure culture *Thielavia terricola* grows vigorously and fruits abundantly when obtaining its sole carbohydrate nutrition from cellulose, indicate that it is a normal soil organism, capable under favorable conditions of growing upon cotton fabric and some other cellulosic materials. It is probable that this species and the classic *Thielavia basicola* are identical, but proof is lacking until Zopf's authentic specimens are available for comparison.

Prevention of Decay in Substructures of Houses on Wet Sites. DILLER, JESSE D. In providing living accommodations for thousands of war workers and their families, many war-housing projects throughout the country were built on sites that are believed to be too wet. In most cases contact of wood with soil has been avoided. However, particularly where outside temperatures go low enough to promote condensation on sills, there is often need for ventilation in houses that have no heating plant under the floor, in order to keep the wood below a dangerous moisture content. A study was made of 21 houses without basements, in 11 locations in the vicinity of Washington, D. C. Substructure wood moisture, relative humidity, and temperature were determined at approximately 3-month intervals for periods of 2 to 3 years. The results indicate that ½ sq. ft. ventilator opening for each 25 linear feet of foundation wall, plus ½ sq. ft. for each 100 sq. ft. of building area is sufficient. Where it is impracticable to provide adequate ventilation and condensation occurs, tests now in the third winter show that it can be prevented and the wood moisture contents kept below the danger point without ventilation, by covering the soil with asphalt roll roofing. (Division of Forest Pathology, Bureau of Plant Industry, Soils, and Agricultural Engineering, Agricultural Research Administration, U. S. Department of Agriculture.)

Artificial Transmission of the Virus of Big Vein of Lettuce. DOOLITTLE, S. P., AND ROSS C. THOMPSON. All of the writers' earlier attempts to transmit the big-vein virus by artificial inoculations were made with expressed juices of diseased leaves, and no infection occurred. Recent experiments, however, have shown that infection is readily secured when freshly extracted juices of roots of big-vein plants are rubbed on the leaves or pricked into the leaves or stem. Fifty-six of 76 lettuce plants inoculated by these methods have been infected. All plants were grown in steam-sterilized pots and soil. The incubation period varied from 36 to 60 days with nearly all affected plants showing symptoms at about 45 days. These periods are about the same as are required for development of symptoms in healthy plants transplanted to infested soil. Drying the roots for 7 days seemed to inactivate the virus. Parallel inoculations, made with juices of mottled leaves of the plants whose roots were used as inoculum, produced no infection. When needle punctures were made through healthy and diseased leaves held in close contact, 1 out of 8 plants showed symptoms within 18 days. This period was so short as to suggest prior contamination of the soil. The experiment is being repeated. All the 80 control plants in the experiments remained healthy. (Division of Fruit and Vegetable Crops and Diseases, Bureau of Plant Industry, Soils, and Agricultural Engineering, Agricultural Research Administration, U. S. Department of Agriculture.)

Organization and Germination of Oospores in Several Species of Pythium. DRECHSLER, CHARLES. Although in their early "lumpy" stage oospores of *Pythium oligandrum* may show only one refringent body, at maturity they commonly reveal 5 to 15 refringent bodies in the finely granular layer surrounding the single reserve globule. If sparingly irrigated after aging 6 months, they often germinate by extending an evacuation tube, 10 to 50 μ long, through which the contents migrate into a vesicle to be fashioned into zoospores. The oospore of *P. periplocum* often produces an evacuation tube 50 to 200 μ long, which conducts the protoplasm into a terminal vesicle. In *P. salpingophorum*, *P. vexans*, and *P. anandrum*, the germinating oospore may deliver its contents into a vesicle, or may produce a sporangium; germ sporangia in the latter 2 species are often citriform and distally papillate. After aging 6 months the large globose resting spore of *P. undulatum* Petersen *sensu* Dissmann, which contains many reserve globules and plural refringent bodies, germinates promptly on shallow irrigation by extending 1 to 3 germ hyphae whereon are borne collectively 1 to 4 ellipsoidal, often distally papillate, and

occasionally proliferous sporangia. From its internal organization, its two-layered wall, and manner of germination, it may possibly represent a parthenospore homologous to the oospore of *P. ostracodes*. (Pathologist, Division of Fruit and Vegetable Crops and Diseases, Bureau of Plant Industry, Soils, and Agricultural Engineering, Agricultural Research Administration, U. S. Department of Agriculture.)

Helminthosporium turcicum Leaf Blight of Corn. ELLIOTT, CHARLOTTE, AND MERLE T. JENKINS. As a result of the epidemic of *Helminthosporium turcicum* leaf blight in 1942, field inoculation experiments were conducted at Beltsville, Maryland, in 1944 to determine the relative susceptibility of inbred lines and crosses of dent corn to this disease. About 6 acres of corn were inoculated twice weekly, beginning the last week in June and ending as plants came into tassel. Spore suspensions from a mixture of 5 isolations of the fungus from corn at Beltsville were sprayed into the central whorl of leaves. Rapid spread of the disease began the last week in July and continued throughout the season. Leaf-blight ratings on 200 inbred lines, 175 single crosses, and 162 double crosses indicate that most lines and crosses are susceptible. NC34, CI.23, K175, Ky114, Mo21A, T49B, T105B, and K155 in one group of 100 and CI.15, CI.16 and T × 206 in a second group of 100 inbred lines were more resistant than any others tested, showing only traces to light infection. Other lines showed moderate to very heavy infection. In general, the resistance of resistant lines was apparent in their hybrids. Some of the more resistant lines also were resistant in the natural epidemic of 1942.

A Comparison of the Agar Plate and Test-tube-dilution Methods for the Preliminary Evaluation of Fungicides. GOTTLIEB, DAVID. A comparison of sensitivity of agar-plate and test-tube-dilution procedures for preliminary assay of fungicides is important. Present investigations reveal that each test gives reproducible values for the toxicity of the chemicals, sufficiently precise for detecting promising materials. However, neither test alone will indicate all materials with good fungicidal activity. For these comparisons the usual agar-plate method has been so altered that the spores are applied to the agar in drops of water from the same collection and at the same spore concentration used in the test-tube-dilution method. Eighty-five different organic compounds were tested against two fungi, *Macrosporium sarcinaeforme* and *Sclerotinia fructicola*, in dosage series at 0, 16, 32, 63, 125, 250, and 500 ppm. and the L.D. 50 values determined. With the former organism 49.5 per cent of the compounds had the same toxic values by both methods. The agar-plate method was more sensitive than the test-tube-dilution method for 35.4 per cent and the test-tube-dilution method more sensitive for 15.3 per cent of the compounds. Similar results were obtained with *Sclerotinia fructicola*. When the L.D. 100 was used for comparison with the agar-plate method, there were still many compounds that gave different toxic values depending on the procedure used. For this reason it may be important to utilize more than one procedure in the preliminary evaluation of chemicals as fungicides.

New Organic Fungicides in the Control of Tomato and Potato Diseases. HEUBERGER, J. W., AND T. F. MANNS. In 1943 it was found that Spergon, Fermate, No. 604, and Dithane did not control early blight on potatoes; adding zinc sulphate-lime (1–½–100) to Dithane increased its protective value over that of Bordeaux and yields were significantly increased by 37 bu. an acre. Research with Dithane on potatoes in 1944 showed the following: (1) addition of lime alone to Dithane did not increase control of early blight or leaf hopper burn; (2) zinc sulphate alone significantly increased control of early blight and hopper burn; (3) zinc sulphate and lime together were not so effective as zinc sulphate alone. In 1944, calcium, sodium, iron, zinc, copper, and lead dimethyl dithiocarbamates (2–100) were evaluated on potato and tomato plants. Zinc dimethyl dithiocarbamate was significantly the best for control of early blight and hopper burn of the potato and of early blight and anthracnose on the tomato; the calcium salt showed considerable promise. Adding zinc sulphate-lime resulted, in general, in significant increases in protective value for the calcium, sodium, and iron salts but not for the zinc, copper, and lead salts. Zinc dimethyl dithiocarbamate was the best of any organic or copper fungicide used for control of hopper burn on potato and of anthracnose on tomato. It was equal to Bordeaux for early blight control on tomatoes and potatoes.

New Developments in Spraying and Dusting Equipment. HOPPERSTEAD, S. L. A brief review of the development and performance of the Speed Sprayer, Vertical Boom Attachments, Cornell Sprayer-Duster, California Sprayer-Duster, and the use of Aerosols was presented. The advantages or disadvantages of the equipments as compared to standard commonly used machines was discussed as well as the recent findings regarding present control of pests, the objectives sought and the future possibilities for improvement. The possibilities of adapting the Aerosol principle for control of field and storage

troubles of commercial crops were advanced and experimentation along these lines encouraged.

Periconia Blight of the Hevea Rubber Tree. IMLE, ERNEST P., AND JOHN A. STEVENSON. A new disease, occasionally causing conspicuous damage to the Hevea rubber tree, has been reported from Mexico (unpublished) by W. J. Martin and from Costa Rica by the writers. An unnamed species of *Periconia*, having exceptionally large spores, was identified on such diseased leaf specimens of *Hevea spruceana* and *H. brasiliensis* collected at Turrialba, Costa Rica. Symptoms consist of leaf spots and leaf, petiole, and twig blight on *H. spruceana* but seem to be confined to leaf spots and blight on *H. brasiliensis*. Leaf spots are circular or elongated along leaf veins and from 2 to 10 mm. or more in diameter. On young leaves the spots often coalesce involving an entire leaflet and causing abscission. Both surfaces of the necrotic spots show the presence of large, dark, septate conidiophores. These, together with their apical cluster of spores, measure 200 to 300 μ tall and are easily visible to the naked eye on close inspection. Infection has been readily obtained on *H. spruceana* and on *spruceana* × *brasiliensis* hybrids by atomizing with a spore suspension and by suspending diseased leaves above susceptible foliage. In one test, spores were being produced on the newly formed lesions 10 days after inoculation.

The Value of Several Fungicides as Sweetpotato Seed and Sprout Treatments. JEFFERS, W. F., AND C. E. COX. Maryland Golden sweetpotatoes dipped in solutions of Borax, Spergon, and compound No. 604, before bedding, produced significantly more sprouts at the first pulling than untreated and mercuric chloride-treated. Total sprouts from 3 pullings show all treatments significantly better than check. Addition of Nu-Film, a rosin-residue sticker, delayed production but significant differences were still obtained. Sprouts from untreated sweetpotatoes were dipped in various solutions at the rate of 1 lb. of material per 10 gal. Six weeks after planting, Fermate plots showed significantly better stand than check; both Fermate and Spergon were better than Semesan Bel at odds of 99: 1. Fusarium-wilt infection was reduced significantly by all treatments. Spergon- and Fermate-treated sprouts yielded significantly better than Thiosan and Semesan Bel at the 5 per cent point and better than the Mycoban (calcium propionate) and untreated plots at the 1 per cent point. Results were not so good when the same treatments were used in a paraffin base.

Elsinoë piri Discovered on Apple and Pear in Western Washington and Oregon. JENKINS, ANNA E., M. J. FORSELL, AND L. W. BOYLE. The conidial stage (*Sphaceloma*) of what is evidently *Eslinoë piri*, causing a leaf and fruit spotting of apple and pear, was discovered in the United States in 1943. It was found in western Washington by the Special Pest Survey of the U. S. Bureau of Entomology and Plant Quarantine. The following year a survey by the Emergency Plant Disease Prevention Project revealed its presence on both apple and pear in western Oregon. At present, so far as is known, the disease is confined to the moist sections of these States and is not known to occur in commercial apple-growing sections. Trees on which the disease was found are in home plantings, generally not of recent origin and practically without cultural attention. The characteristic fruit and leaf spot was seen on old apple varieties, names now unknown, as well as on Ortley, Grimes Golden, and King, and also on apple seedlings. Late yellow varieties and seedlings with light-colored fruit appear to be particularly susceptible. As many as 100 spots, up to 2 mm. in diameter, have been counted on a single small fruit; characteristically, these were present chiefly on the blush side. An equal number of spots, 0.5 mm. to 1 mm. in diameter, have been noted on a more or less limited area of a single leaf blade. Leaf spots may reach 3 mm. in diam. The assembled data indicate that the apple and pear disease has been present in western Washington and Oregon for an extended period.

Further Studies on Bacterial Leaf Blight and Stalk Rot of Corn. JOHNSON, A. G., ALICE L. ROBERT, AND LILLIAN CASH. The bacterial leaf blight and stalk rot of corn, previously reported from Alabama and Virginia, has now been reported also from Georgia, Texas, Kansas, and Nebraska. In some Kansas fields it was reported as rather common in 1943 and 1944, although not particularly destructive in either year except in localized spots. In the recent reports, the stalk-rot symptoms have been less common than originally reported from Alabama. The leaf symptoms have been very similar but the severity of the attacks has been lighter than in Alabama. The causal organism is very similar to if not identical with *Pseudomonas alboprecipitans*, originally isolated from *Setaria lutescens*. The organism has been shown pathogenic on leaves of dent corn, sweet corn, wheat, barley, rye, and oats; and to some extent on sorghum, Sudan grass, *Setaria lutescens*, and *S. geniculata*. The best infections were obtained when greenhouse temperatures were relatively high. Seed of dent corn and sweet corn, inoculated with water suspensions of

the organism, produced seedlings with primary lesions from which the typical organism was isolated. Water suspensions of the organism also caused the typical stalk rot in field and greenhouse.

Observations on the Bacterial Canker of Cowpea. LEFEBVRE, C. L., AND HELEN S. SHERWIN. Burkholder in 1944 described *Xanthomonas vignicola* as the cause of bacterial canker of cowpeas, while in the same year Hoffmaster suggested that it may be caused by *Bacterium vignae*. The writers have made isolations from specimens of Blackeye cowpeas sent from Texas, and from Whippoorwill and Chinese Red cowpeas collected in Florida. Both yellow and white bacteria were obtained, but only the yellow organism proved to be pathogenic. When grown on different media, the yellow organism agreed with the description given by Burkholder for *X. vignicola*. The first symptoms observed after inoculation are extremely variable, depending somewhat on method of inoculation. On primary leaves, small white spots 1–2 mm. in diameter develop. The tissue in these small spots shrivels, drys, and often drops out, producing a shot-hole effect. A halo usually forms around these spots and the invaded tissue becomes water-soaked. The lesions may enlarge to an inch or more in diameter before the leaf wilts. Often the primary and trifoliate leaves wilt without any apparent lesions. On stems, cankers may be the first observable symptoms, and cankers may appear anywhere on stems. Inoculations have shown that varieties differ greatly in relative resistance.

Races of Helminthosporium turcicum. LEFEBVRE, C. L., AND HELEN S. SHERWIN. Cultures of *Helminthosporium turcicum* isolated from common Sudan grass, Atlas sorghum, Johnson grass, and corn differed in their ability to infect the host testers employed. Two cultures from common Sudan grass and one from Atlas sorghum were pathogenic on Sudan grass and Gooseneck sorghum, but all failed to infect corn (Hy × 540). Four of the cultures from corn infected common Sudan, while two did not, all six being highly pathogenic on corn (Hy × 540). The culture from Johnson grass caused heavy infection only on its own host. Hence, these ten cultures represent four distinct parasitic races. The fact that many of the isolates from corn are able to produce heavy infection on common Sudan grass may help to explain why Sudan grass is always so heavily infected by *H. turcicum* when grown in Eastern United States. On the other hand, although only a few cultures from Sudan grass and sorghum were used, these failed to infect corn. This may account for the frequent absence of the fungus on corn growing close to heavily infected Sudan grass.

A Red Leaf Disease of Field and Sweet Corn. MANNS, T. F., AND C. E. PHILLIPS. In working with leaf blights on many strains of hybrid and open-pollinated corn in 1943 and 1944, we observed a disease, new to Delaware, that we are calling the red leaf disease of corn. It is a systemic disease, characterized in its early stages by brilliant red foliage, turning in its later stages to a brilliant purplish-red, involving the whole plant. There are no necrotic lesions, nor any quick wilting areas. Plants from 2 feet in height to full-size were infected. The ear, though present, never completed kernel formation. In this respect the disease causes total loss. In one plot of 44 strains at Georgetown, 35 sources were infected, that is 79.3 per cent; the amount of infection varied from 1.7 to 11.7 per cent with an average of 4.9 per cent. In 1943, at Newark, 37 per cent of a sweet-corn planting was affected. The cause of the disease is unknown to the writers. Our review of corn diseases shows none similar in symptoms. Cultures of surface-disinfected leaves (1–3000 alcoholic bichloride of mercury) frequently gave an abundant bacterial growth having colonies with a metallic lustre similar to that of *Bacterium pruni*. We have made no inoculations. Is the disease bacterial, virus, or an inherited breakdown?

Chlorosis in Seedlings of Hevea brasiliensis. MARTIN, W. J. Less than 0.1 per cent of the Hevea seedlings growing in nurseries in Mexico and Guatemala has been observed to exhibit a partial chlorosis, ranging in severity from a few well-defined spots on a few leaves to almost complete chlorosis of most of the leaves on some affected plants. With very young leaves the condition appears as lighter green spots, mostly with irregular margins. As the leaves mature the affected parts usually lose all chlorophyll and become yellow or white. In severe cases the young stem may appear yellowish green or streaked with yellow. Different leaf flush cycles on the same plant may show different degrees of chlorosis. The chlorosis has been propagated through patch budding; 30 of the 32 buddings, made with buds from affected seedlings placed on normal green seedlings, developed shoots showing the condition. Different degrees of chlorosis appeared among buddings made from the same budwood stick. In 1 of 6 cases, a bud from a normal green seedling, budded on an affected seedling, developed a shoot with a similar chlorosis on a single leaf in the third leaf flush cycle. This suggests that the condition may be transmissible.

Salts as Antidotes to Copper in its Toxicity to Fungi. MARSH, P. B. Spore-germination experiments with *Stemphylium* sp., *Curvularia* sp., and *Penicillium* sp., after the man-

ner of earlier experiments with *Sclerotinia fructicola* (Phytopath. 35: 54–61, 1945) reveal pronounced antidoting effects of calcium chloride toward the toxicity of copper sulphate. Experiments with *Stemphylium* indicate that the minimum ratio of calcium to copper necessary for observation of the antidoting response increases with increasing copper concentration. At a given copper concentration KCl is less effective than $CaCl_2$. Germination of spores of *Stemphylium* in water suspension on a film of copper hydrogenated resinate may be raised from zero to over 90 per cent by the use of an antidoting salt.

The Use of Easter Lily Bulb Scales for Evaluating Fungicides. McCLELLAN, W. D., AND NEIL W. STUART. The results obtained when Easter lily scales (*Lilium longiflorum*) are treated with various fungicides and growth substances for the control of scale rot caused by *Fusarium oxysporum* f. *lilii*, suggest their use as a test object for the evaluation of fungicides. The use of Easter lily scales has these advantages: all scales from one clon have the same genetic constitution; clons differ in susceptibility to scale rot, so that both susceptible and resistant clons may be employed; resistant clons provide a measure of the growth-promoting properties of the materials tested; bulbs can be used at any time of the year if properly handled; the organism readily infests the sand on which the scales are placed and the lesions it produces on the scales can be seen with ease; the materials to be tested can be applied as a dust, a suspension, or a solution; the equipment is simple (Phytopath. 34: 966–975, 1944); and the method is rapid, gives reproducible results, requires very little space, and measures small differences accurately because of the low variability between replicates.

Observations on Lima-bean Scab in Puerto Rico. McCUBBIN, W. A. Lima-bean scab (*Elsinoë phaseoli*) occurs in Puerto Rico on cultivated and semi-wild Lima beans, and has been frequently encountered in the inspection of pod Lima beans offered for shipment to the mainland since 1930. Observations in Puerto Rico during 1935–39 indicate that, following pod infection, there is a rapid expansion of the scab spot, which at this stage is slightly raised, remains uncolored, and produces a copious but transient crop of superficial conidia; that color appears upon an early and complete transition from the conidial to the ascosporic stage with little, if any, increase in spot size thereafter; that pod infection was obtained with difficulty from ascospore suspensions; that the conidia may be largely responsible for field spread; and that in frozen and unfrozen scabby pods subjected to moist decay the asci and ascospores appeared to become disorganized along with the host tissues, suggesting the possibility that the fungus may not be adapted to carry over in dead plant parts, and thus might have difficulty in bridging the interseason gap in cold regions. (Bureau of Entomology and Plant Quarantine, Agricultural Research Administration.)

Virus of Cucumber Mosaic Withstands Desiccation in Leaf Tissue. McKINNEY, H. H. When finely cut leaf tissue had become "dry" in laboratory atmosphere at 18.5° to 23° C, virus activity could not be detected, but when dried at 35° C and stored over $CaCl_2$ in a disiccator at 23° C, there was slight activity after 58 days. However, when the tissue was dried and stored at 1° to 2° C, over $CaCl_2$, there was much activity after 153 days. In the laboratory, in humid climates, leaf tissue does not become completely dry, as it does in a desiccator. It appears that slow incomplete drying at laboratory temperatures favors reactions of plant constituents, possibly enzymes, that are deleterious to the virus, and that these reactions can be reduced or possibly eliminated in a very dry atmosphere at suitable temperatures.

A Leafspot of Cowpea and Soybean, Caused by a New Species of Helminthosporium. OLIVE, LINDSAY S., DOUGLAS C. BAIN, AND C. L. LEFEBVRE. A species of *Helminthosporium*, apparently heretofore undescribed, was found causing severe spotting of cowpea leaves in Louisiana in August, 1944. Since then specimens of cowpeas, as well as soybeans, diseased by the same fungus, have been received from North Carolina, South Carolina, and Florida. The fungus was obtained in culture, and inoculations were carried out on several varieties of cowpea and soybean. All plants became infected, but the cowpeas sustained the greater amount of damage. Two parasitic races have been isolated. Race 1, originally isolated from cowpea leaves, causes a severe spotting of cowpea leaves and a light spotting of soybean leaves; whereas race 2, originally isolated from soybean leaves, produces a light spotting of soybean leaves and few to many small dots of little consequence on cowpea leaves. The fungus is a rather atypical species of *Helminthosporium*, with long tapering conidia, formed singly or in chains under proper conditions of temperature and moisture, at the tips of long, dark-brown conidiophores. We are applying to the disease the common name of target-spot, with reference to the concentric zonation in each leaf spot on the cowpea, which is the chief host.

Distribution of Races of Tilletia foetida and T. caries in Relation to the Wheat Improvement Program in the United States. RODENHISER, H. A., AND C. S. HOLTON. Fifteen

races of *Tilletia foetida* and 16 of *T. caries* have been identified from 369 bunt collections from 35 States in the United States, 6 States in Mexico, and 2 Provinces in Canada. The most prevalent and widely distributed races of *T. foetida* are L–1, L–2, L–3, and L–4; and of *T. caries* T–1, T–2, and T–4. The first 3 and 2 of each group, respectively, are pathogenic only on the old commercially grown varieties. Several other races of both species, pathogenic on the newer varieties bred primarily for smut resistance, are rather widely distributed. Apparently the distribution and prevalence of specific wheat varieties are the most important factors governing the distribution and prevalence of particular races. It seems evident from wheat varietal tests with the above races that the so-called Hope or H-44 factors supply adequate resistance for the spring wheats, while the combined factors from Oro and Martin supply the necessary factors for resistance in the winter wheats. Both Ridit and Oro possess factors governing resistance to all of the races thus far identified in collections from Mexico. (Cooperative investigations between the Division of Cereal Crops and Diseases, U. S. Department of Agriculture and the Washington and Idaho Agricultural Experiment Stations.)

Meadow Nematodes as the Cause of Root Destruction. STEINER, G.

Why Soil Fumigation? STEINER, G.

Phloem Necrosis Research During 1944. SWINGLE, ROGER U., B. S. MEYER, AND CURTIS MAY. Resistance tests have been in progress since 1942 on seedlings and clones of a few American elms (*Ulmus americana*) suspected of being resistant to phloem necrosis because of their survival in areas where the disease has occurred for many years. Results as yet are not conclusive but they indicate that many of these seedlings and clones are resistant to phloem necrosis. Some natural hybrids between *Ulmus fulva* and *Ulmus pumila* seem to be resistant also. Preliminary physiological investigations of inner bark indicate important differences in oxidizing enzyme activity, oxygen consumption, and water relations between diseased and healthy phloem. Electron microscope studies failed to reveal any differences between phloem exudates from diseased and healthy trees. Epidemics of phloem necrosis are now developing across Missouri and in eastern Kansas. The disease area is now known to include the southern halves of Ohio, Indiana, Illinois, and Missouri, eastern Kansas, western West Virginia, Kentucky, western Tennessee, and northern Mississippi. Throughout this area losses among both wild and planted elms were extremely heavy in 1944. (Division of Forest Pathology, Bureau of Plant Industry, Soils, and Agricultural Engineering, Agricultural Research Administration, U. S. Department of Agriculture.)

Occurrence and Distribution of Physiologic Races of Ustilago hordei in the United States. TAPKE, V. F. In a study of 444 collections of barley covered smut from 33 States, 13 distinct physiologic races of *Ustilago hordei* were isolated by means of the 8 differential varieties, Excelsior (C.I. 1248), Hannchen (C.I. 531), Himalaya (C.I. 1312), Lion (C.I. 923), Nepal (C.I. 595), Odessa (C.I. 934), Pannier (C.I. 1330), and Trebi (C. I. 936). Race 6 was by far the most common. It occurred in 272 of the 444 collections and was found in 28 of the 33 States. In California and Washington, however, race 5 was very prevalent, occurring in 42 of 45 collections from the former and in 21 of 29 from the latter. In the winter-barley region, races 1 and 6 were common. Races 1, 5, and 6 comprised 86.5 per cent of the total collections. The knowledge of the relative importance of these 3 races and of the occurrence and distribution of all 13 races should appreciably facilitate breeding for resistance against the covered smut of barley, especially since we now have an effective artificial method of inoculating the seed with *U. hordei*.

Control of Bean Rust by Fungicide Dusting and Spraying. ZAUMEYER, W. J., AND M. C. GOLDSWORTHY. Sulphurs (wettable and liquid), dithiocarbamates, and chlorinated naphthoquinone proved to be highly efficient in greenhouse experiments in the control of rust infections. Copper compounds were not so effective as the above materials. Liquid lime-sulphur, chlorinated naphthoquinone (604), and disodium ethylene bisdithiocarbamate (Dithane) proved especially effective in eradicating the fungus from infected bean plants (24-hour infection). In field studies, dusting with finely ground (325-mesh) sulphur at the rate of 20–25 pounds of sulphur per acre, before and immediately following the field observation of primary rust infections, controlled the disease; large reductions in yield were observed in unprotected plantings. The field dusting was done during the evening, or the quiet hours of day or night, or in the early morning. Dusting was not done during the hours when dew or precipitation was present on the vines because of the hazard of spreading bacterial blight. (Division of Fruit and Vegetable Crops and Diseases, Bureau of Plant Industry, Soils, and Agricultural Engineering, Agricultural Research Administration, U. S. Department of Agriculture, Beltsville, Maryland.)